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Fishery Bulletin

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LIFE HISTORY PATTERNS IN MARINE FISHES AND THEIR CONSEQUENCES FOR FISHERIES MANAGEMENT

PETER B. ADAMS[1]

ABSTRACT

Natural selection operates at the life history level to maximize the number of surviving offspring. Life history characteristics will vary in consistent patterns to meet this constraint. When theoretical patterns in life histories were investigated in terms of *r* and *K* selection and compared with actual trends in life history characteristics of fishes, the agreement between observed and predicted trends was significant. The effects of harvesting on stocks with these life history trends were investigated and it was found that *K* selected type species would be highly sensitive to overfishing and, once depleted, recovery would require a long time.

The ecological and genetic properties of a species are intimately linked. The morphological and reproductive characteristics, population sizes, and genetic frequencies of species are adjusted to their environments by natural selection. Species inhabiting different environments show different patterns of life history characteristics. The relationship among habitat, ecological strategies, and population parameters has been termed *r* and *K* selection (MacArthur and Wilson 1967) and/or optimal life histories (Gadgil and Bossert 1970). This body of theory is based on the assumption that natural selection operates on these characteristics in order to maximize the number of surviving offspring produced. Under an environmental regime with a large component of unpredictable, nonselective, mortality an organism will allocate a larger portion of its resources to reproductive activities (an *r* strategist). Conversely the optimal allocation of resources for a population subjected to a high proportion of predictable, selective mortality will be toward increasing individual fitness, frequently through competitive ability (a *K* strategist). With the number and variability of factors operating on any particular species, no species is going to be an *r* or *K* strategist in an absolute sense. A species will only occupy a relative position on the *r* and *K* continuum.

In fisheries biology, the value of comparative studies of life history parameters has long been recognized (Holt 1962; Beverton 1963; Cushing 1971; Alverson and Carney 1975). These life history parameters should vary in a consistent pattern which can be predicted from the theory of *r* and *K* selection. In this paper, these predictions are tested with life history parameters from major groups of marine fishes. The theory has implications for management, particularly when fisheries are in the initial stages of development.

THEORY OF *r* AND *K* SELECTION

The theory of *r* and *K* selection is based on two assumptions about the allocation of a population's resources between competitive and reproductive functions (Pianka 1974; Gadgil and Bossert 1970; Schaffer and Gadgil 1975). The first is that there is a positive relationship between the amount of resources spent on an offspring and the fitness of that offspring. The second assumption is that any species only has a fixed amount of resources available. This results in an inverse relationship between the number of offspring produced and their average fitness. The criterion for success in natural selection is the number of surviving offspring that a parent produces (Crow and Kimura 1970). Therefore, the best reproductive strategy is a compromise between two conflicting demands: production of the largest possible total number of offspring (*r* selection), and production of offspring with the highest possible fitness (*K* selection). The particular point of compromise for any species will be a function of the selection factors operating on that species and would be that species' position on the *r* and *K* continuum.

The second part of the theory concerns the relationship between these life history strategies and

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the habitat the species occupies (Southwood et al. 1974; Southwood and Comins 1976). If mortality factors in an environment are variable and/or unpredictable, then their effects are likely to be less selective in terms of population size or of the phenotype involved. Under these circumstances, individual competitive fitness is of relatively less importance. The best strategy would be to place maximal resources into reproduction and produce as many offspring as possible (r selection).

The contrasting situation is an environment in which mortality factors are stable and/or predictable. Mortality under these circumstances will result in strong selection for individual fitness and there will be pronounced differences between their effects on different phenotypes. In these stable environments, the optimal strategy would be to produce offspring with substantial competitive ability (K selection). Due to the previously assumed relationship between fitness per offspring and the number of offspring produced, this also means the production of fewer offspring.

The two situations described above are end points of a spectrum. Species will always have a number of different selective pressures operating on them, both spatially and temporally. This is particularly evident in aquatic organisms which characteristically go through several life history stages. This again emphasizes that the concept of r and K selection should be applied only in a comparative sense. Finally, comparisons must be made between species of a similar ecological nature. Comparisons between species of different ecological types is meaningless since fundamentally different types of selective factors will be operating in those cases.

r AND K SELECTION IN MARINE FISHES

Natural selection will favor nonreproductive activities at the expense of reproductive activities only when they enhance reproduction at later stages in the life history and thereby maximize overall survival (Crow and Kimura 1970). Changes in allocation of a species' resources from reproductive to competitive activities will only occur in habitats where competitive activities enhance the survival of future offspring. The result of this is that organisms under different selection pressures will have characteristic life history patterns. An r selected species will have life history strategies which tend toward productivity. The K selected species will have life strategies which tend toward efficient exploitation of a specific limiting resource (Pianka 1974). Therefore, specific combinations of population parameters can be identified as being characteristic of an r strategist, while the opposing combination would be characteristic of a K strategist.

A species which is exposed to a large component of nonselective or catastrophic mortality (i.e., an r strategist) would be selected for characteristics that would increase productivity. Increasing productivity through reproductive activity generally implies: 1) early maturity, 2) rapid growth rates, 3) production of larger numbers of offspring at a given parental size, and 4) maximum production of offspring at early age (Gadgil and Bossert 1970). Other characteristics which are results of the allocation of large portions of resources to reproductive activity are: 1) small body size, 2) high rates of mortality, and 3) shorter life span (Pianka 1974; Gadgil and Solbrig 1972). In terms of commonly measured population parameters in fishery biology, an r selected species would have: 1) a low age at first maturity, 2) a high value of k from the von Bertalanffy growth equation, 3) a small L_∞ from the von Bertalanffy growth equation, 4) high rates of instantaneous natural mortality (M), and 5) low maximum age.

Even in environments with predictable mortality sources, increased allocation of resources to competitive activities will only occur when two prerequisites are met (Schaffer and Gadgil 1975). The first is that reproductive potential increases with some function of age. The second is that there is some additional mortality risk associated with reproduction. Under these assumptions, the attributes associated with a K strategist would be: 1) delayed maturity, 2) reduced growth rates, 3) low mortality rates, 4) large body size, and 5) longer life span. Again in terms measured in fishery biology, a K selected species would have: 1) a high age at first maturity, 2) a low k from the von Bertalanffy growth equation, 3) a large L_∞ from the von Bertalanffy growth equation, 4) low M, and 5) a high maximum age.

Using these life history correlates of r and K selection (summarized in Table 1), it is possible to predict the signs of a correlation matrix between life history parameters (Table 2). The predicted matrix can be compared with actual matrices calculated using Spearman's rank correlation coefficient. This coefficient only assumes that the observed data are mutually independent and come

TABLE 1.—Summary of hypothetical *r* and *K* correlates in life history parameters of fishes.

Characteristics	*r* selected	*K* selected
Body size, L_∞[1]	Small	Large
Maximum age	Low	High
Age at first maturity	Low	High
Natural mortality, *M*	High	Low
Growth rate, k[1]	High	Low

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 2.—Predicted signs of correlation matrix of life history parameters in fishes.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	*M*	k[1]
Body size, L_∞[1]	1.0	+	+	−	−
Maximum age		1.0	+	−	−
Age at first maturity			1.0	−	−
Natural mortality, *M*				1.0	+
Growth rate, k[1]					1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

from a continuous bivariate population (Hollander and Wolfe 1973).

RESULTS

Life history parameters were gathered from the literature for several major groups of marine fishes. Often there were multiple sets of data for the same species from different locations. Each set of values was used as a separate data case. The literature citations for the actual parameters are listed by group in Appendix I. Correlation matrices were calculated for the following groups of fish: 1) herring and anchovies, Clupeidae and Engraulidae (Table 3), 2) salmons, Salmonidae (Table 4), 3) cods, Gadidae (Table 5), 4) rockfishes, Scorpaenidae, genus *Sebastodes* (Table 6), and 5) flatfishes, Pleuronectiformes (Table 7).

All of the observed correlations agree with the predicted correlations in sign (Table 8). Of the observed correlations, 40 of a possible 46 (or 87%) were significantly different from zero at a 5% probability level. If the observed correlation agreement of coefficients were distributed ran-

TABLE 3.—Correlation coefficients between life-history parameters for herring and anchovies (families Clupeidae and Engraulidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	*M*	k[1]
Body size, L_∞[1]	1.0	0.846	0.816	−0.746	−0.720
		(0.001)	(0.001)	(0.001)	(0.001)
Maximum age		1.0	0.904	−0.797	−0.763
			(0.001)	(0.001)	(0.001)
Age at first maturity			1.0	−0.702	−0.732
				(0.001)	(0.001)
Natural mortality, *M*				1.0	0.876
					(0.001)
Growth rate, k[1]					1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 4.—Correlation matrix between life-history parameters for salmons (family Salmonidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	*M*	k[1]
Body size, L_∞[1]	1.0	0.765	0.728	−0.785	−0.730
		(0.001)	(0.032)	(0.001)	(0.002)
Maximum age		1.0	0.776	−0.737	−0.674
			(0.020)	(0.003)	(0.004)
Age at first maturity			1.0	−0.644	−0.812
				(0.084)	(0.013)
Natural mortality, *M*				1.0	0.896
					(0.001)
Growth rate, k[1]					1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 5.—Correlation matrix between life-history parameters for cods (family Gadidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	*M*	k[1]
Body size, L_∞[1]	1.0	0.795	0.833	−0.647	−0.666
		(0.002)	(0.001)	(0.022)	(0.001)
Maximum age		1.0	0.737	−0.654	−0.702
			(0.014)	(0.028)	(0.008)
Age at first maturity			1.0	−0.715	−0.658
				(0.035)	(0.008)
Natural mortality, *M*				1.0	0.950
					(0.001)
Growth rate, k[1]					1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 6.—Correlation matrix between life-history parameters for rockfishes (family Scorpaenidae, genus *Sebastodes*). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	k[1]
Body size, L_∞[1]	1.0	0.662	0.456	−0.490
		(0.019)	(0.088)	(0.075)
Maximum age		1.0	0.612	−0.567
			(0.030)	(0.040)
Age at first maturity			1.0	−0.651
				(0.021)
Growth rate, k[1]				1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 7.—Correlation matrix between the life-history parameters for flatfishes (order Pleuronectiformes). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	M	k[1]
Body size, L_∞[1]	1.0	0.755 (0.001)	0.956 (0.001)	−0.291 (0.156)	−0.619 (0.005)
Maximum age		1.0	0.824 (0.001)	−0.355 (0.142)	−0.808 (0.001)
Age at first maturity			1.0	−0.630 (0.014)	−0.732 (0.001)
Natural mortality, M				1.0	0.367 (0.098)
Growth rate, k[1]					1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 8.—Summary of the number of agreements between predicted and observed correlation coefficients among life-history parameters within selected taxonomic groups.

Level of agreement	Number in agreement	Number possible	Percent in agreement
Sign	46	46	100
5% probability level	40	46	87
1% probability level	31	46	67

domly (i.e., p = probability of agreement = 0.5, and q = probability of disagreement = 0.5), then the number of agreements would follow a binomial distribution. The binomial test (Hollander and Wolfe 1973) can be used to test the hypothesis that the number of agreements between the predicted and observed correlations differs from the number that would have occurred randomly. The number of agreements is significantly different than would have occurred randomly (z = 4.86, P<0.001), when only correlations that were significant at the 5% level were used.

RESPONSE OF r AND K SELECTED SPECIES TO HARVESTING

The interaction of life history characteristics will have a strong affect on the response of a species to fishing pressure. The Beverton and Holt yield per recruit equation estimates the yield that can be harvested from the growth of a cohort. The model assumes that fish growth is described by the von Bertalanffy growth curve and that mortality processes are exponential (Beverton and Holt 1957; Ricker 1975). The biological parameters in the model are: 1) M, the instantaneous rate of natural mortality, 2) W_∞, the mean asymptotic weight which corresponds to L_∞, 3) k, the von Bertalanffy growth coefficient, and 4) t_λ, the maximum age of a fish. From r and K selection, we can predict how these parameters will vary. Consider a situation with three hypothetical species: one species will be more r selected, another species will be more K selected, and another will be intermediate between the first two. The biological parameters will vary as shown in Table 9. Beverton and Holt yield per recruit curves were calculated for a constant age at first capture (t_r = 4.2 yr) with varying fishing mortality (Figure 1), and for a constant fishing mortality (F = 0.25) with a varying age at first capture (Figure 2).

The yield per recruit analysis points up that there are specific differences in fisheries based on r or K selected species. In fisheries based on K selected species, the maximum yield per recruit would occur at a lower level of fishing mortality and at a later age at first entry than in fisheries based on r selected species. The curves also indicate that K selected species would be much more sensitive to overfishing both in terms of fishing mortality and age at first entry.

The surplus production model of Schaefer combines reproductive and mortality functions into one parameter (Ricker 1975). The biological parameters in this model are B_∞, the maximum stock size (or carrying capacity in weight), and k, the instantaneous rate of increase of the stock at densities approaching zero. Again these parameters can be predicted for the three hypothetical species from r and K selection (Table 10). In the surplus production model analysis (Figure 3), the r selected species have the highest productivity. As in the yield per recruit analysis, the maximum yield occurs at a lower fishing mortality for the K

TABLE 9.—Biological parameters for use in yield per recruit analysis for three hypothetical r and K selected species.

Biological parameters	r selected species	Intermediate species	K selected species
Natural mortality, M	0.30	0.20	0.10
Mean asymptotic weight, W_∞	641 g	1,141 g	1,641 g
von Bertalanffy growth coefficient, k	0.22	0.14	0.07
Maximum age, t_λ	13 yr	20 yr	35 yr

TABLE 10.—Biological parameters for surplus production model analysis for three hypothetical r and K selected species.

Biological parameters	r selected species	Intermediate species	K selected species
Maximum stock size (B_∞)	1.54×10^8g	2.04×10^8g	2.54×10^8g
Rate of increase (k)	0.912	0.612	0.312

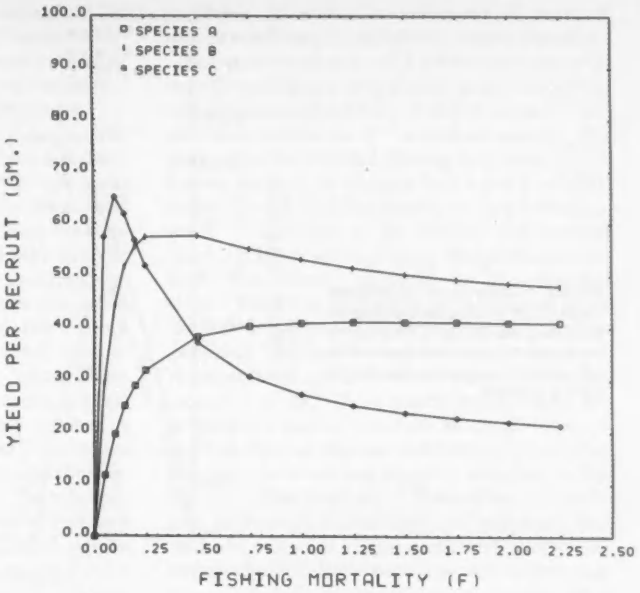

FIGURE 1.—The effect of different levels of fishing mortality with constant age of recruitment (4.2 yr) on yield per recruit of three hypothetical fish species demonstrating the range of r and K selection.

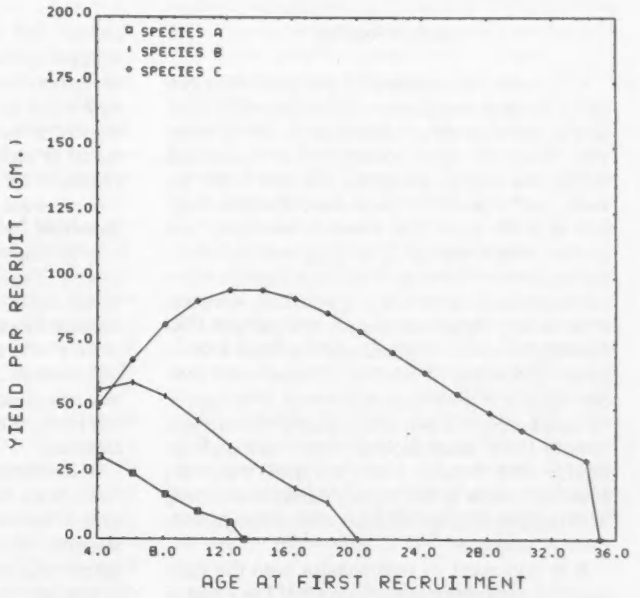

FIGURE 2.—The effect of different mean ages of recruitment at constant fishing mortality ($F = 0.25$) on yield per recruit of three hypothetical fish species demonstrating the range of r and K selection.

selected species than for the r selected species. The K selected species is reduced to levels lower than the maximum sustainable yield by overfishing much more rapidly than the r selected species.

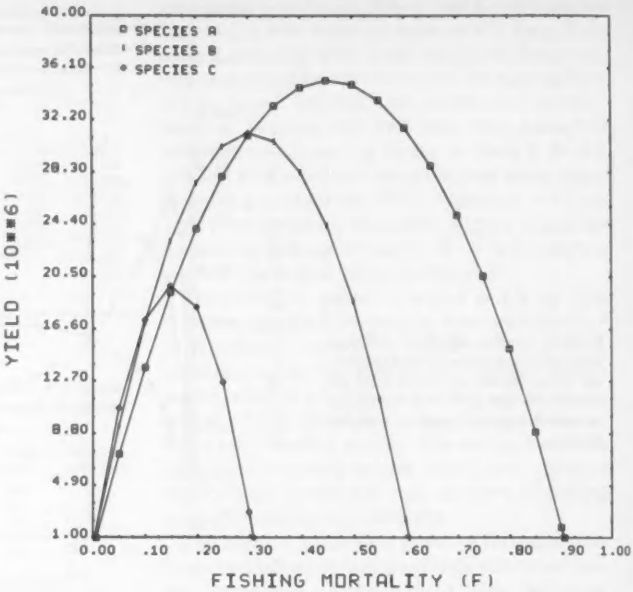

FIGURE 3.—Maximum equilibrium yields ($\times 10^6$ g) from Schaefer surplus production curves as a function of fishing mortality for three hypothetical fish species demonstrating the range of r and K selection.

DISCUSSION

Life history parameters vary in consistent patterns. These patterns are explainable and predictable by the theoretical constructs of r and K selection. This is not a particularly new or unique idea in fisheries biology. Beverton and Holt (1959) investigated a positive relationship between body size and life span and between mortality and growth rates. Cushing (1971) suggested that there is a negative relationship between degree of density dependent regulation and fecundity. Alverson and Carney (1975) have suggested a positive relationship between body size and the time when a cohort maximizes its biomass. In population ecology, similar relationships have been investigated for zooplankton (Allan 1976), plants (Gadgil and Solbrig 1972; MacNaughton 1975), and animals (Smith 1954; Bonner 1965). All these empirical observed trends in life history parameters, along with the trends described here, are consistent with r and K selection.

It is important to reemphasize here the comparative nature of r and K selection. The r and K continuum is a model and as such occurs only in an idealized sense. The idealized r selected species occurs in an ecological vacuum with no density effects and no competition. The idealized K selected species occurs in a completely saturated ecosystem where densities are high compared with carrying capacities and competition for resources is intense. The problem of applying this model to any real situation is not a trivial one. Species are not simply subjected to a single selective pressure, or even to a single set of selective pressures. Because of this, r and K concepts should only be applied in a comparative sense between groups of species that have some degree of functional similarity. No species is r selected or K selected in an absolute sense; it is only relatively more r selected or K selected than some other reference species. This theory will only have value in a situation where the population dynamics of one member of a species group are fairly well understood.

The results of the model analysis give several indications about the reaction to harvesting pressure of species which are more or less r or K selected. Fisheries based on more r selected species will be more productive. They can be fished at younger ages and at higher levels of fishing mortality. Given a minimum population size, these fisheries should also have a quicker recovery from overfishing. Species which are more r

selected are likely to be strongly influenced by physical forces in the environment (Pianka 1974). Relationships of this type, e.g., between anchovies and upwelling, should be important considerations in management plans for these species.

Fisheries based on more *K* selected species will have a high maximum yield per recruit, but there will be fewer fish. Maximum equilibrium yield will occur at later ages of entry into the fishery and at lower levels of fishing mortality. These fisheries would be more susceptible to overfishing and stock depletion. Besides these species' sensitivity to overfishing, more *K* selected species are much more likely to have sophisticated life history mechanisms (Pianka 1974) which would have to be recognized in a management plan. These mechanisms might include parental care systems such as nesting or live births, mating systems, or territoriality. The more *K* selected species are much more likely to have strong interspecific relationships, usually competitive ones. The relationship between competition and harvesting has been dealt with by Larkin (1963) and Tanner (1975). Additional density independent mortality (fishing mortality) increases the advantage for the population with a higher population growth rate (i.e., more *r* selected). Therefore, even low levels of fishing pressure can destabilize a previously stable competitive pair and result in decline of the harvested species. Interestingly, the opposite result is also possible; harvesting pressure can stabilize a previously unstable species pair as Slobodkin (1962) found with experimental populations of hydra.

Fisheries based on more *r* selected species are likely to be of a boom and bust nature. Although in some years catches in these fisheries will be very large, they will be characterized by erratic production levels. The most efficient form of harvesting these fisheries will be fleets which are capable of switching between a number of target species relatively quickly.

Fisheries based on more *K* selected species, in contrast to the boom and bust nature of *r* selected fisheries, will be characterized by relatively stable population sizes and therefore catch levels. Given some initial measure of year class strength, possibly through larval or prerecruitment surveys, the prediction of future catches from that fishery could be made with a fair degree of accuracy. However, once fisheries based on these species become overfished, it would require a long period for the stock to rebuild to levels which can support economical profitable fisheries. An extremely *K* selected species would only be suitable for trophy fisheries.

Fisheries based on *r* and *K* selected species have been discussed in a comparative sense, but predation (in the case of a fishery, human predation) will also have effects on an individual species. The gene pool of any species is going to contain within it some range of variation of both *r* and *K* selected traits. The effects of increasing fishing mortality, which is assumed to be density independent (Cushing 1975), on life history characteristics has been theoretically analyzed by Roughgarden (1971). The general effect is an increase in selective advantage for the *r* selected proportions of the gene pool. This would mean an increase in growth rates, reduced age at first maturity, and greater fecundity at age. These trends will be more conspicuous in species that are relatively more *K* selected. Species that are more strongly *r* selected are likely to have less range of variation in this direction. One example of these effects of predation pressure is a comparison of lake trout, *Salvelinus namaycush*, populations under heavy predation pressure from the freshwater harbor seal, *Phoca vitulina*, to populations in nearby lakes without seals (Power and Gregoire 1978). The lake trout populations which were preyed upon by seals had faster growth rates, small maximum body size, reduced maximum age, lower age at sexual maturity, and greater individual fecundity compared with populations in lakes without seals. Growth and maturation rates of certain seal species have also increased where populations have been reduced by fisheries (Sergeant 1973). These affects can be attributed to changes in selection pressure resulting from sustained harvesting.

In summary, *r* and *K* selection seems to have been an important evolutionary trend on marine fish populations. The basic hypotheses are confirmed by the data presented here. The result of patterns in population parameters which arise from *r* and *K* selection is that different management strategies would be appropriate. The value of this approach is likely to be in initial stages of development of a fishery. As a fishery becomes more developed and more specific information becomes available, a more refined management strategy would become possible.

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APPENDIX I: LITERATURE CITATIONS FOR POPULATION PARAMETERS BY SPECIES

Herring and Anchovies, Families Clupeidae and Engraulidae

Clupea harengus—Lea 1919; Sund 1943a, b; Jensen 1947; Fridriksson 1950, 1951-61; Alander 1950; Tibbo 1956, 1957a, b; Hannerz 1956; Gilis 1957-61; Smith 1957; Day 1957; Cushing 1959; Nielsen 1960; Burd 1962; Parrish and Craig 1963; Postuma 1963; Bowers 1963.

C. pallasii—Hanamura 1953; Tester 1955; Ricker 1958; Tanaka 1960; Ayushin 1963; Motoda and Hirano 1963.

Sprattus sprattus—Robertson 1938; Molander 1943; Faure 1950; Elwertowski 1957-60.

Sardinops caerulea—Silliman 1943; Phillips 1948; Mosher and Eckles 1954; Clark and Marr 1955; Murphy 1966; Culley 1971.

S. melanosticta—Tanaka 1960; Tokai Regional Fisheries Research Laboratory 1960.

S. neopilchardus—Blackburn 1950.

S. ocellata—Davies 1958; De Jager 1960; Culley 1971.

Sardina pilchardus—Hodgson and Richardson 1949; Bough 1952; Hodgson 1957; Larrañeta 1960; Cushing 1961; Culley 1971.

Sardinella aurita—Postel 1955; Rossignol 1955; Richardson et al. 1960; Ben-Tuvia 1960; Beverton 1963.

S. longiceps—Nair 1960.

Engraulis encrasicholus—Fage 1920; Furnestin 1945.

E. japonicus—Hayashi and Kondo 1957; Watanabe 1958; Tanaka 1960; Hayashi 1961.

E. mordax mordax—Clark and Phillips 1952; Miller et al. 1955; Miller and Wolf 1958; Culley 1971.

Cetengraulis mysticetus—Barrett and Howard 1961.

Salmons, Family Salmonidae

Coregonus clupeaformis—Hart 1931; Hile and Deason 1934; Kennedy 1943, 1953; Ricker 1949.
Cristivomer namaycush—Kennedy 1954.
Leucichthys artedii—Hile 1936.
L. kiyi—Deason and Hile 1947.
Oncorhynchus kisutch—Shapovalov and Taft 1954; Drucker 1972.
O. nerka—Foerster 1968; Van Cleve and Bevan 1973.

Cods, Family Gadidae

Boreogadus saida—Beverton and Holt 1959.
Gadus callarias—Beverton and Holt 1957; Taylor 1958.
G. macrocephalus—Ketchen 1964.
G. minutus—Menon 1950.
G. morhua—Fleming 1960; Pinhorn 1969; Clayden 1972.
G. virens—Beverton and Holt 1959.
Melanogrammus aeglefinus—Raitt 1939; Beverton and Holt 1957.
Merluccius merluccius—Beverton and Holt 1959.

Rockfishes, Family Scorpaenidae, Genus *Sebastodes*

Sebastodes crameri—Phillips 1964.
S. diploproa—Phillips 1964.
S. entomelas—Phillips 1964.
S. flavidus—Phillips 1964.
S. goodei—Phillips 1964.
S. jordani—Phillips 1964.
S. miniatus—Phillips 1964.
S. paucispinis—Phillips 1964.
S. pinniger—Phillips 1964.
S. saxicola—Phillips 1964.

Flatfishes, Order Pleuronectiformes

Citharichthys sordidus—Arora 1951.
Eopsetta jordani—Ketchen and Forrester 1966.
Hippoglossus platessoides—Powles 1965, 1969; MacKinnon 1973.
H. vulgaris—Beverton and Holt 1959.
Isopsetta isolepis—Hart 1948.
Pleuronectes platessa—Beverton and Holt 1959.
Pseudopleuronectes americanus—Dickie and McCracken 1955.
Solea vulgaris—Beverton and Holt 1957.

SPECIES OF *MUNIDOPSIS* (CRUSTACEA, GALATHEIDAE) OCCURRING OFF OREGON AND IN ADJACENT WATERS

JULIE W. AMBLER[1]

ABSTRACT

Twelve species of *Munidopsis* (Decapoda: Crustacea: Galatheidae) were collected from the continental slope, Cascadia Basin, and Tufts Abyssal Plain off Oregon and in adjacent waters. Three new species are described: *Munidopsis cascadia, M. tuftsi,* and *M. yaquinensis*. One specimen, *Munidopsis* sp., closely related to *M. bairdii*, is described but unnamed, pending capture of more specimens. *Munidopsis chacei* is synonymized with *M. bairdii* and *M. geyeri* is synonymized with *M. subsquamosa*. The ranges of seven previously described species are now extended to Oregon and Washington: *M. aries, M. bairdii, M. beringana, M. ciliata, M. latirostris, M. subsquamosa,* and *M. verrucosus*. The 12 species occurred between 950 and 4,194 m; 3 species were found on the continental slope (950-2,189 m); 9 species were found on Cascadia Basin (1,900-3,025 m); and 3 species were found on Tufts Plain (3,390-4,194 m). Species composition on Cascadia Basin differed from east to west. The highest densities (number of specimens per trawl) occurred at the base of the continental slope and 40 miles farther west. One species, *M. latirostris*, contributed 73.0% of the total number of specimens, and three other species (*M. bairdii, M. ciliata*, and *M. subsquamosa*) contributed an additional 20.2%. The species collected also occur in the Atlantic (*M. bairdii, M. aries*), tropical Pacific and Indian (*M. ciliata*), tropical Pacific (*M. latirostris*), Arctic (*M. beringana*), southern temperate Pacific (*M. verrucosus*), or are cosmopolitan (*M. subsquamosa*), or are endemic on Cascadia Basin (*M. cascadia, M. yaquinensis*), and on Tufts Plain (*M. tuftsi*).

Species of *Munidopsis* are found from intertidal waters to the abyssal plains of the deep sea. *Munidopsis polymorpha* is found in saltwater lakes in caverns connected to the sea in the Canary Islands (Dinkins 1969). *Munidopsis crassa*, the deepest known species, was found at 4,700 m in the Bay of Biscay (Sivertson and Holthuis 1956). Recently, an unidentified *Munidopsis* sp. has been found near submarine hot springs near the Galapagos (Corliss and Ballard 1977). In general, the genus is found in the deep sea with about half of the known species occurring deeper than 800 m (Doflein and Balss 1913).

In the eastern Pacific Ocean, the first *Munidopsis* species were collected off Chile by the *Challenger* (Henderson 1888) and in the eastern tropical Pacific by the *Albatross* (Faxon 1895). Benedict (1902) described additional new species collected by the *Albatross* off southern California and the Galapagos, and in the Bering Sea. Since then, Bahamonde (1964) and Khodkina (1973) have found new species off Chile, and Pequegnat and Pequegnat (1973) described a new species off Baja California and Costa Rica from the *Albatross* and *Galathea* collections. Little work has been done on *Munidopsis* occurring off the west coast of the United States. Schmitt (1921), in a key to *Munidopsis* species found off California, included *M. verrilli, M. hystrix, M. aspera*, and *M. quadrata*. Haig (1956) modified this key to include *M. depressa*.

This paper discusses the taxonomy and distribution of 12 *Munidopsis* species collected mainly off Oregon from 950 to 4,194 m. These depths include the lower slope and the abyssal plains of Cascadia Basin and Tufts Plain (Figure 1). Among species found off Oregon, only *M. quadrata* has previously been collected from the west coast of the United States. Three new species are described: *M. cascadia, M. tuftsi,* and *M. yaquinensis*. One species, *Munidopsis* sp., is described but left unnamed until more specimens become available to elucidate its relationship to *M. bairdii*. The ranges of seven previously described species are extended to Oregon: *M. bairdii, M. beringana, M. ciliata, M. aries, M. verrucosus, M. latirostris,* and *M. subsquamosa*.

METHODS

A total of 803 specimens were collected from 146

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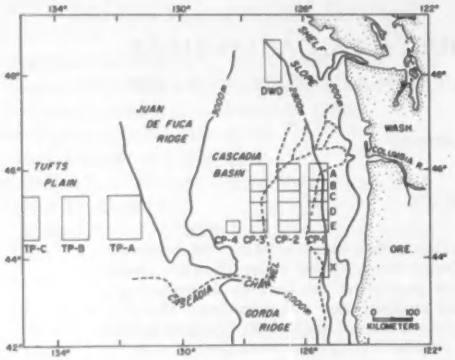

FIGURE 1.—Stations sampled in Cascadia Basin and Tufts Plain, off Oregon and Washington.

benthic otter trawls (OTB, OT) and beam trawls (BMT) during 13 yr of sampling by Andrew G. Carey, Jr., School of Oceanography, Oregon State University. On Cascadia Basin, samples were collected on three north-south lines ranging from the CP-1 line (Figure 1) at the base of the continental slope to the CP-3 line 80 mi farther offshore. The base of the continental slope varies from 1,900 m on the Astoria Fan at CP-1-A to 2,816 m at CP-1-E. At the base of the continental slope farther south, between lat. 43° and 44° N, a small trench occurs in which depths reach 3,000 m. Stations become deeper both to the south and to the west in Cascadia Basin. One sample was taken from Gorda Ridge off California, south of Cascadia Basin. Ten tows were made in northern Cascadia Basin on Nitinat Fan off Washington, during a study of deepwater dumpsites (Carey et al. 1973). Three areas (TP-C, TP-B, TP-A) were sampled on Tufts Plain. Station abbreviations are as follows: NAD = Newport hydrographic line, mainly slope stations; CP = Cascadia Basin, off Oregon; TP = Tufts Plain; and DWD = Deepwater dumpsite, northern Cascadia Basin, off Washington.

The beam trawl is a semiquantitative sampler (Carey and Heyamoto 1972), with a rigid frame of steel skids connected by a 3 m aluminum pipe, with a collecting net of 4.1 cm stretch mesh lined with 1.3 cm mesh net. The otter trawl is a 7 m semiballoon Gulf of Mexico shrimp trawl with 4.1 cm stretch mesh with a 1.3 cm mesh liner. Samples were preserved at sea in 10% formaldehyde and sorted in the laboratory.

The specimens were examined through a dissecting microscope and measured with vernier calipers usually to the nearest millimeter. The following measurements were used (Figure 2):

Carapace length (CL) = tip of rostrum to middle of posterior margin of carapace.
Anterior width of carapace = width between anterolateral spines.
Posterior width of carapace = width at posterior margin of carapace.
Rostrum length = tip of rostrum to rostrum base, which lies on an imaginary line between the bases of the ocular peduncles.
Cheliped length = tip of chela to articulation between ischium and sternum.
Chela length = tip of chela to articulation between chela and carpus, on the ventral side.
Eyespine length = tip of eyespine to proximal end of cornea.

Incomplete synonymies are given for each species. References include original description, first redescription if the original description was very short, first figure, and all synonyms.

The specimens from Oregon State University (OSU) were compared with those borrowed from the U.S. National Museum (USNM), the Museum of Comparative Zoology at Harvard (MCZ), and from Texas A&M University (TAMU). Specimens of each species are cataloged in the Oregon State University Benthic Invertebrate Museum (OSUBI). The holotypes and a few paratypes of the new species were deposited at the U.S. National Museum.

MUNIDOPSIS WHITEAVES 1874

Munidopsis Whiteaves 1874:212 (original description); Smith 1885:493 (synonomy with *Galacantha*); Milne-Edwards and Bouvier 1894:271, 1897:63 (redescriptions); Faxon 1895:81-83 (synonomy with *Orophorhynchus, Elasmonotus, Galathodes,* and *Anoplonotus*); Chace 1942:69 (synonomy with *Galacantha*).

Galathodes Milne-Edwards 1880:53 (original description); Milne-Edwards and Bouvier 1894:276, 1897:94 (redescriptions).

Orophorhynchus Milne-Edwards 1880:58 (original description); Milne-Edwards and Bouvier 1894:283, 1897:110 (redescriptions).

Elasmonotus Milne-Edwards 1880:60 (original description); Milne-Edwards and Bouvier 1894:279, 1897:98 (redescriptions); Henderson 1888:165 (synonomy with *Galathopsis*).

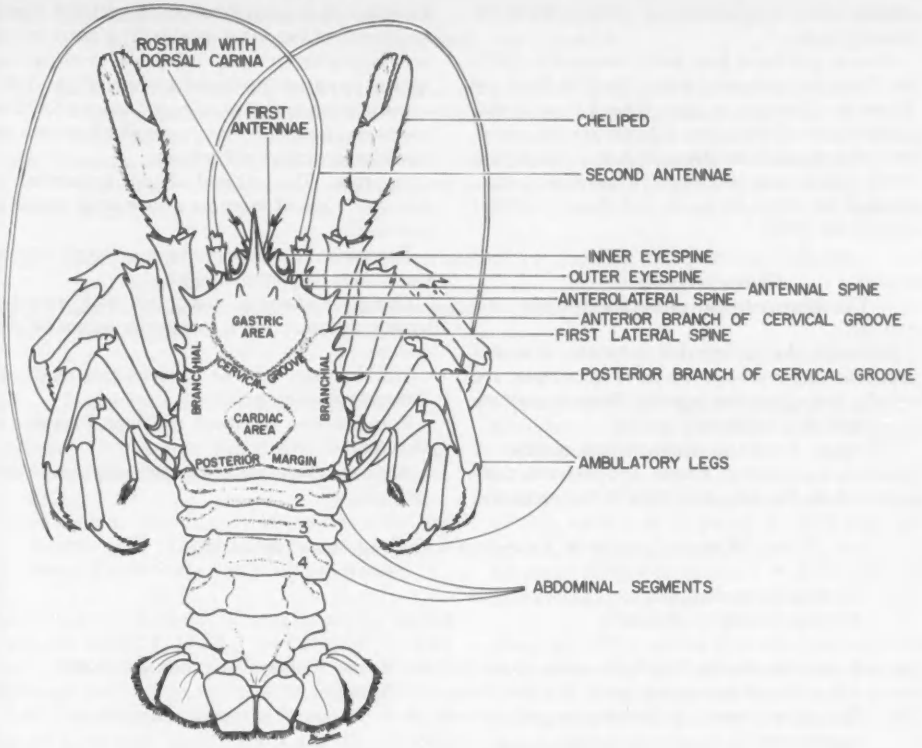

FIGURE 2.—Generalized drawing of the genus *Munidopsis*.

Anoplonotus Smith 1883:50 (original description).
Galathopsis Henderson 1885:417 (original description).
Galacantha Milne-Edwards 1880:52 (original description); Henderson 1888:166 (redescription, argues for separate genus); Milne-Edwards and Bouvier 1894:268, 1897:55 (redescriptions).

Diagnosis.—Integument heavily calcified; carapace longer than wide, covered with spines, sometimes with setae, and with rugae often in transverse rows; dorsal surface of carapace with well-defined cardiac and gastric areas, gastric area separated from branchial area by cervical groove; anterolateral borders of carapace usually spinose or dentate but occasionally entire; anterior border of carapace sometimes with small supra-antennal spine or tooth, never with a long supraorbital spine; eyes small, unfaceted, and devoid of pigment; ocular peduncle sometimes extended beyond cornea as a spine (eyespine); rostrum well developed, triangular or spatulate; antennular peduncle with short flagellum; antennal peduncle four jointed, usually with long flagellum; chelipeds either longer or shorter than next three ambulatory legs, epipodite present sometimes on chelipeds and occasionally on ambulatory legs; moderate number of large eggs, a few millimeters in diameter.

The genus *Munidopsis* (including *Galacantha*) has about 140 species with 112 of them covered in checklists by Doflein and Balss (1913) and 101 in a checklist by Benedict (1902). The genus has been divided into five groups called either genera, subgenera, or groups (Henderson 1888; Milne-Edwards and Bouvier 1894; Alcock 1901; Tirmizi 1966). Faxon (1895) and Chace (1942) recommended a single genus *Munidopsis* because many

species show characteristics intermediate between groups.

Several extensive keys exist. Benedict's (1902) key describes all specimens in the U.S. National Museum collection at that time. Chace (1942) wrote a key to the western Atlantic species, which has been updated by Pequegnat and Pequegnat (1970, 1971). Other extensive keys were constructed by Milne-Edwards and Bouvier (1894) and Alcock (1901).

Characteristics of Taxonomic Importance for Species

Although the antennular peduncle, antennal peduncle, and merus of the third maxilliped are usually drawn for new species, these characters are rarely used to identify species.

Carapace. Presence, absence, and number of spines on the anterior, lateral, and posterior margins and on the dorsal surface of the carapace. Presence of the antennal spine variable among specimens of the same species. The basic type of ornamentation (ridges, tubercles, crenulations, spines, setae) on the dorsal surface. Slight differences in ornamentation, size, and spacing found on specimens from different geographic locations are considered varietal differences.

Rostrum. The general shape: triangular or rounded. Lateral margins armed with spines or unarmed.

Eyespines. Presence or absence; length in relation to cornea; sharp or blunt.

Chelipeds. Length compared with carapace length; ornamentation, especially spines on segments.

Walking legs. Not as important as chelipeds. General ornamentation.

Epipodites on chelipeds and legs. Presence or absence.

Abdomen. Presence or absence of spines on dorsal surface.

Key to Species of *Munidopsis* off Oregon and Washington

1a.	No epipods on chelipeds	2
1b.	Epipods present on chelipeds	5
2a.	Eyespines absent; one large spine on second, third, and fourth abdominal segments; frontal and lateral margin of carapace forms a right angle	*quadrata*
2b.	Eyespines present; abdomen unarmed; spine or tooth present at anterolateral corner of carapace	3
3a.	Wide, triangular rostrum; posterior margin of carapace unarmed	*aries*
3b.	Narrow rostrum with or without lateral spines; posterior margin of carapace armed with 1 to 10 spines	4
4a.	Rostrum with 2-6 lateral spines, posterior margin of carapace armed with 3-10 (usually 4-6) spines; chela with 2 inner spines	*bairdii*
4b.	Rostrum with no lateral spines; posterior margin of carapace armed with one spine; chela without two inner spines	sp.
5a.	Eyestalks extend beyond eye as definite, sharp spines	6
5b.	Eyestalks extend beyond eye as blunt processes	11
6a.	Two eyespines present, a longer inner spine and a short outer spine	*ciliata*
6b.	Only inner eyespine present	7
7a.	Rostrum wide, not triangular, with dorsal carina, rounded at end	*yaquinensis*
7b.	Rostrum triangular, with dorsal carina and pointed at end	8
8a.	Carapace and legs covered densely with setae; lateral margins of carapace without spines	*cascadia*
8b.	Carapace and legs not covered densely with setae; spines on lateral margins of carapace	9

9a. Thin, unarmed rostrum strongly upturned ..... *beringana*
9b. Triangular rostrum armed with spines or teeth, not upturned 10

10a. Rostrum armed laterally with two to four small spines; carapace covered with crenulated (margin cut into rounded scallops) tubercles; eyespines long, anterolateral spine about same size as first lateral spine ..... *tuftsi*
10b. Rostrum armed laterally with minute teeth; carapace covered with semicircular scalelike tubercles with long setae; eyespines short; anterolateral spine larger than first lateral spine ..... *subsquamosa*

11a. Rostrum triangular without dorsal carina; large spine on second, third, and fourth abdominal segments ..... *verrucosus*
11b. Rostrum wide at base, nearly parallel to eyestalks, with dorsal carina; abdomen with no large spines ..... *latirostris*

Munidopsis quadrata Faxon 1893

Munidopsis quadrata Faxon 1893:1888 (original description); Faxon 1895:97 (redescription), pl. 23, fig. 1, 1e.
Elasmonotus quadratus Milne-Edwards and Bouvier 1894:281-282 (under discussion of genus *Elasmonotus*, key to *Elasmonotus*).

Material.—OSUBI 00170, gravid female, 11 mm CL, stn NAD 11, 44°39.0′ N, 124°59.9′ W, BMT 312, 950 m; OSUBI 00171, male, 13 mm CL, stn Waldpt., 44°21.7′ N, 125°07.9′ W, OT 27, 1,000 m; OSUBI 00182, gravid female, 12 mm CL, male, 11 mm CL, stn NAD 12, 44°38.8′ N, 125°09.1′ W, OTB 360, 1,170 m; OSUBI 01580, 2 specimens, stn DWD 5, 48°38.1′ N, 126°58.1′ W, BMT 9, 2,189 m.

Distribution.—The range of *Munidopsis quadrata* extends from off Destruction Island, Wash., to Tres Marias Islands, Mexico, at depths usually between 620 and 1,571 m; it has also been found at 86 and 110 m, off Wilmington, Calif., and Los Coronados Islands, respectively (Rathbun 1904). These shallow records (86 and 110 m) seem unlikely when compared with the usual depth range of 620-1,571 m, although other species of *Munidopsis* do occur on the Continental Shelf. *Munidopsis quadrata* occurs on the continental slope off Oregon and on the Nitinat Fan off Washington at 950-2,189 m, which extends the known depth range.

Munidopsis aries (Milne-Edwards 1880)

Orophorhynchus aries Milne-Edwards 1880:58 (original description); Milne-Edwards and Bouvier 1897:111-113 (redescription), pl. 9.
Munidopsis aries. Benedict 1902:316 (genus changed to *Munidopsis*).

Material.—USNM 171346, female, 43 mm CL, stn CP-2-E, 44°38.4′ N, 126°42.0′ W, BMT 270, 2,850 m; OSUBI 00169, female, 29 mm CL, stn CP-3-E Channel, 44°44.4′ N, 127°22.1′ W, BMT 359, 3,025 m. The holotype was not examined.

Remarks.—This species is known from only three specimens—the type and two Oregon specimens (Table 1). *Munidopsis sundi* and *M. albatrossae*, both giant species, are most similar to *M. aries* in shape and ornamentation of the carapace.

The description of *M. aries* (Milne-Edwards and Bouvier 1897) fits the Oregon specimens except for the chelipeds. In the Oregon specimens, the merus of the cheliped has four small spines at the anterior border and a row of small spines along the dorsal ridge; the carpus has four or five small spines on the dorsal surface with two or three of these at the anterior border. Milne-Edwards and Bouvier (1897) described two denticles at the anterior border of the merus and the carpus. They did not describe the inner margin of the merus of the third maxilliped. In the Oregon specimens three

TABLE 1.—Morphometry of *Munidopsis aries*. Data on holotype from Milne-Edwards and Bouvier (1897).

Measurement (mm)	Holotype	USNM 171346	OSUBI 00169
Carapace length	20	43	29
Rostrum length	5.1	12	8
Anterior carapace width	9.7	18	14
Posterior carapace width	10.5	26	18
Width at widest part of carapace	14	29	19
Cheliped length	18	37	24
Rostrum length/carapace length	0.26	0.28	0.28
Cheliped length/carapace length	0.90	0.86	0.83

small spines occur along the posterior half of this inner margin.

Distribution.—*Munidopsis aries* appears to be a rare, deepwater species. The type is from near Bequia in the Caribbean Sea (lat. 13°N, long. 61.1° W) at 2,912 m. The Oregon specimens were collected at 2,850 m in Cascadia Basin and at 3,025 m in Cascadia Channel.

Munidopsis bairdii (Smith 1884)

Galacantha bairdii Smith 1884:356 (original description).
Munidopsis bairdii. Smith 1886:649 (redescription) pl. 5, fig. 2.
Munidopsis chacei. Kensley 1968:288 (original description) fig. 1.

Material.—Holotype, USNM 5717, female, 45 mm CL, *Albatross* stn 2106, 37°41.3′ N, 73°3.3′ W, 2,740 m; USNM 10801, male, *Albatross* stn 2573, 40°34.3′ N, 66°09′ W, 3,188 m; USNM 171344, male, 48 mm CL, male, 41 mm CL, stn CP-2-B, 45°34.5′ N, 126°18.5′ W, BMT 156, 2,661 m; OSUBI 00193, female, 28+ mm CL, stn CP-2-E, 44°43.4′ N, 126°27.5′ W, OTB 90, 2,772 m; OSUBI 00192, 6 specimens, stn CP-2-C, 45°20.8′ N, 126°37.7′ W, BMT 264, 2,750 m; OSUBI 00194, female, 22 m CL, stn CP-2-D, 44°53.7′ N, 126°33.4′ W, BMT 162, 2,774 m; 51 uncataloged specimens, smallest ovigerous female 43 mm CL.

Remarks.—The characteristics of *Munidopsis chacei* Kensley, are within the range of variation of *M. bairdii* and, therefore, *M. chacei* is here considered a synonym of *M. bairdii*. As noted by Kensley (1968), *M. chacei* and *M. bairdii* differ in the number of spines of the gastric and cardiac areas and on the posterior margin, and the ratio of dactyl to propodal length of the ambulatory legs. However, the range of variation of these characteristics in our specimens of *M. bairdii* includes those observed for *M. chacei* (Table 2).

Munidopsis columbiana Pequegnat and Pequegnat is a closely related species, with the following differentiating characteristics: antennal spines present in *M. columbiana*, absent in *M. bairdii*; abdominal segments with spines in *M. columbiana*, absent in *M. bairdii*; and inner margin of merus of third maxilliped with five to eight teeth in *M. columbiana*, three teeth in *M. bairdii*, and two to four teeth in our specimens.

TABLE 2.—Selected spine counts of *Munidopsis chacei* and *M. bairdii* from their type descriptions, compared with data from 46 Oregon specimens.

Item	Gastric area	Cardiac area	Posterior margin
M. chacei:			
Kensley (1968)	5	4	4
M. bairdii:			
USNM 5717	6	3	10
USNM 10801	5	3	4
Faxon (1895)	4	1	5
Oregon specimens	3-5	2-4	4-6

Pequegnat and Pequegnat (1971) mention two other characteristics, but these do not separate the two species. In their key, the presence of more than seven spines on the carapace separates *M. columbiana* from *M. bairdii*. In the Oregon specimens, the number of spines on the carapace ranges from 5 to 11. The number of lateral spines on the rostrum is not a distinguishing characteristic. *Munidopsis columbiana* can have from two to six lateral spines, but usually has four. The type of *M. bairdii* has six lateral spines. In the Oregon specimens the number of spines ranges from two to six, but usually is four.

Distribution.—*Munidopsis bairdii* occurs at depths of 2,377-2,940 m in Cascadia Basin. It has been previously collected in both the Atlantic and Pacific Oceans: Cape Sable to Cape May (Smith 1886); Cape Hatteras to Nantucket (Smith 1884); off Panama (Faxon 1895); and off the west coast of the Cape Peninsula or Cape Point, South Africa (Kensley 1968).

Munidopsis sp. (Figure 3)

Munidopsis sp. USNM 171345, male, 20 mm CL, stn NAD 17, 44°31.2′ N, 125°15.5′ W, OT 23, 1,829 m.

Remarks.—*Munidopsis* sp. closely resembles *Munidopsis bairdii*, but is distinctly different in some characters. More specimens are needed to verify species status. The form differs from *M. bairdii* in having no lateral spines on the rostrum, a shorter rostrum, only one spine on the posterior margin, rugae on carapace much less pronounced, hairs on carapace thicker, shorter eyespines extending just beyond the cornea, and the chelae not armed with two inner spines. However, *Munidopsis* sp. has four spines on the gastric area and three on the cardiac area, which are within the range found for *M. bairdii*.

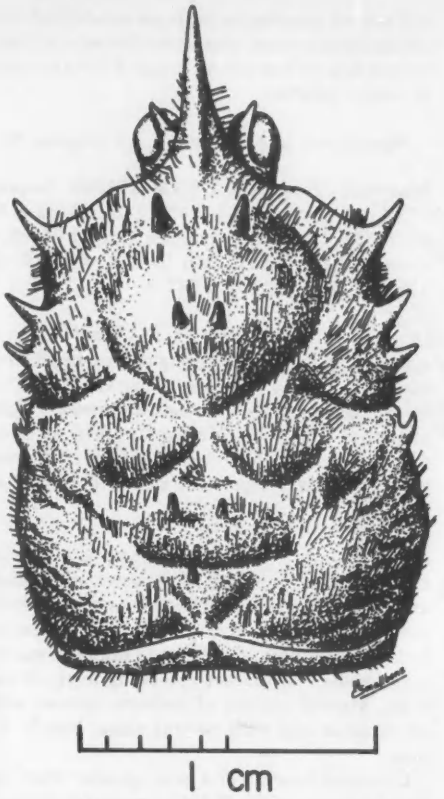

FIGURE 3.—*Munidopsis* sp. (similar to *Munidopsis bairdii*) USNM 171345, dorsal view of carapace.

Distribution.—*Munidopsis* sp. has only been collected from the lower continental slope at 1,829 m, which does not overlap with the depth range of *M. bairdii* (2,377-2,940 m).

Munidopsis ciliata Wood-Mason 1891

Munidopsis brevimana Henderson 1885:414 (original description); Henderson 1888:154 (redescription), pl. 17, fig. 1, 2.

Munidopsis ciliata Wood-Mason 1891:200 (original description); Faxon 1895:84 (synonymy with *M. brevimana*, comparison with *M. nitida*); Faxon 1895:81-82 (*M. ciliata* because genus synonomy caused prior usage of *M. brevimana*), pl. 18, fig. 3.

Material.—MCZ 4540, female, 27 mm CL, *Albatross* stn 3392, 7°5.5′ N, 79°40.0′ W, 2,324 m; MCZ 4541, male, 19 mm CL, *Albatross* stn 3393, 7°15.0′ N, 79°37.0′ W, 1,867 m; USNM 171342, female, 13 mm CL, stn CP-1-A, 45°55.3′ N, 125°36.1′ W, BMT 194, 2,030 m; USNM 171343, 13 specimens, stn CP-2-A, 45°52.5′ N, 126°40.8′ W, BMT 154, 2,666 m; OSUBI 00188, male, 15 mm CL, stn CP-1-E, 44°39.8′ N, 125°36.4′ W, BMT 184, 2,875 m; OSUBI 00189, 33 specimens, stn CP-2-D, 44°53.7′ N, 126°33.4′ W, BMT 162, 2,774 m; OSUBI 01581, females, 16 mm CL, stn CP-2-A, 45°48.3′ N, 126°28.2′ W, BMT 158, 2,651 m; OSUBI 01578, female, 12 mm CL, stn CP-2-C, 45°18.6′ N, 126°31.5′ W, BMT 265, 2,750 m.

Comparative material.—*Munidopsis nitida*: USNM 21287, female, 21 mm CL, *Albatross* stn 2140, 17°36.2′ N, 76°46.1′ W, 1,768 m. *Munidopsis verrilli*: Holotype, USNM 20556, female, 22 mm CL, *Albatross* stn 2923, 32°40.5′ N, 117°31.5′ W, 1,504 m.

Remarks.—The Oregon specimens differ from the *Albatross* specimens by the shorter, stouter spines on the carapace and legs; shorter setae covering the carapace and legs; rostrum with a narrower base; and no extra spine between the anterolateral and antennal spines, as sometimes occurs in the *Albatross* specimens (Figure 4). A small ventral spine occurs behind the large inner eyespine on the Oregon specimens. Carapace sculpturing is similar in all specimens. I conclude that the observed differences are racial or varietal rather than specific. All specimens are from the Indian and Pacific Oceans.

Munidopsis ciliata is closely related to *M. nitida* Milne-Edwards, but has a more sculptured carapace. Faxon (1895) suggested the differences may be racial or varietal rather than specific. *Munidopsis nitida* has only been found in the Atlantic Ocean (Milne-Edwards 1880; Pequegnat and Pequegnat 1970). Because of the distinct differences in carapace sculpture, I consider *M. ciliata* and *M. nitida* to be separate species.

Both *M. ciliata* and *M. nitida* are closely related to *M. verrilli* Benedict, but differ in that *M. verrilli* has no epipods on the chelipeds or walking legs, whereas *M. ciliata* and *M. nitida* have epipods on only the chelipeds; *M. verrilli* has two spines on the crest of the chela and two spines on the inner edge of the merus of the cheliped, whereas *M. ciliata* and *M. nitida* do not; *M. verrilli* does not

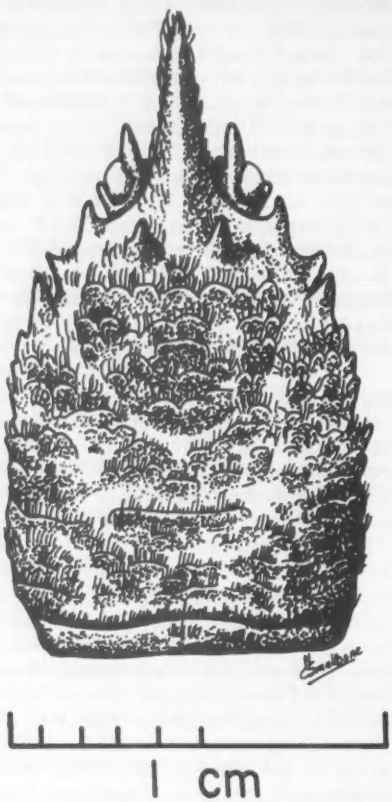

FIGURE 4.—*Munidopsis ciliata*, dorsal view of carapace.

have an inner spine on the third segment of the antennae, which is present in *M. ciliata* and *M. nitida*; and the cheliped is 1.5 times as long as the carapace length in *M. verrilli*, but about the same length in *M. ciliata* and *M. nitida*.

Distribution.—*Munidopsis ciliata* occurs in the eastern part of Cascadia Basin from 2,030 to 2,875 m, off Panama (Faxon 1895) and off the Arrou Islands, Indonesia, (Henderson 1888) in the Pacific Ocean, and the Bay of Bengal, Indian Ocean (Wood-Mason 1891; Alcock 1901). It occurs deeper than *M. verrilli*, which has only been reported off California from San Diego to the Pioneer Seamount at depths of 805-1,618 m (Goodwin 1952). No *M. verrilli* have been found at these depths off Oregon. Goodwin (1952) found *M. verrilli* on rock samples. In one beam trawl (BMT 162) off the Oregon coast, a log was collected at 2,724 m on which there were 33 *M. ciliata*, 67% of the total *M. ciliata* caught.

Munidopsis yaquinensis n. sp. (Figure 5)

Material.—Holotype, USNM 171340, female, 17.4 mm CL, stn CP-3-A, 45°57.1′ N, 127°32.9′ W, BMT 321, 2,763 m; Paratypes: OSUBI 01583, 6 males, 12-13 mm CL, stn CP-1-A, 45°56.5′ N, 125°52.5′ W, BMT 251, 2,377 m.

Diagnosis.—A small species, 12-17 mm CL; large spatulate rostrum with strong carina, small stout eyespines hidden by rostrum; carapace with no spines but covered with small transverse ridges; antennal and anterolateral points of front carapace margin separated by semicircular margin; ambulatory legs with strong anterodorsal carinae.

Description.—Rostrum wide, spatulate, with crenulated edges, base of rostrum with notch around cornea; dorsal surface of rostrum sparsely covered with setae, strong dorsal median carina from anterior part of rostrum to center of gastric area, median carina not extending to tip of rostrum; ventral surface of rostrum covered with small setae and with central ridge; length, 4.9 mm.

Carapace length (17.4 mm) greater than anterior carapace width (8.3 mm), posterior carapace width (11.5 mm), or largest width of carapace (12.2 mm); frontal margin with antennal and anterolateral points separated by semicircular border; lateral margins without spines, forming raised rounded margin; single ridge at posterior border, unarmed; carapace surface covered by small ridges with setae on anterior side, ridges strongly transverse except for those on anterior branchial regions, two larger ridges with crenulated edges on anterior gastric area.

Sternum covered by very small ridges with long setae.

Abdomen unarmed, covered with setae, very slight ridges on somites two and three.

Ocular peduncle movable, with a small, stout, inner eyespine covered by rostrum, eyespine a little longer than length of unpigmented cornea.

Basal segment of antennular peduncle with small anterodorsal spine and anteroventral, jagged, stout tooth.

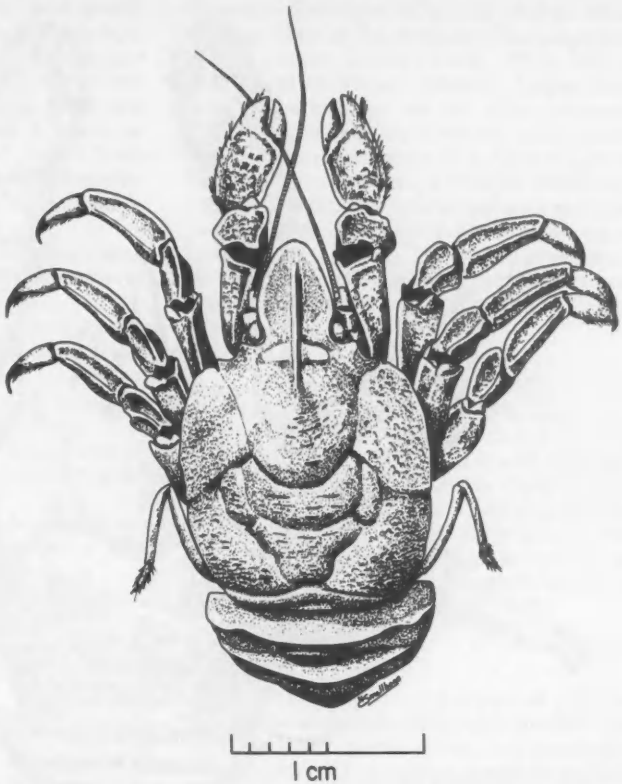

FIGURE 5.—*Munidopsis yaquinensis*, new species, female holotype, dorsal view.

Basal segment of antennal peduncle with two stout teeth; second, third, and fourth segments without teeth or spines; anterior fourth segment with outer rounded extension.

Inner margin of third maxilliped smooth.

Chelipeds with epipodites, chelipeds covered with very small ridges with setae, carpus with strong inner ridge, merus triangular with strong dorsal ridge, right finger length 47% of chela length (6.4 mm), right cheliped length 19.0 mm. Pereiopods without epipodites, covered sparsely with only short setae; propodus, carpus, and merus triangular in cross section, with prominent ridges on anterodorsal side.

Remarks.—The seven Oregon specimens are similar in all important characteristics, with the exception of an OSUBI 01583 specimen, which has an extra long, apparently deformed, rostrum with notched sides.

Munidopsis yaquinensis differs distinctly from all other known species. It most closely resembles *M. platirostris* (Milne-Edwards and Bouvier 1897) and *M. livida* (Pequegnat and Pequegnat 1971).

Etymology.—*Munidopsis yaquinensis* is named for the Oregon State University oceanographic ship RV *Yaquina*.

Distribution.—Occurs at 2,763 and 2,377 m in Cascadia Basin.

Munidopsis cascadia n. sp. (Figure 6)

Material.—Holotype, USNM 171338, female, 54 mm CL, stn CP-1-E, 44°35.5′ N, 125°35.4′ W, OTB 112, 2,810 m; Paratypes: USNM 134658, male, 45 mm CL, stn CP-1-E, 44°46.2′ N, 125°01.8′ W, OTB 49, 2,800 m; USNM 171339, female, 38 mm CL, stn CP-2-A, 45°59.1′ N, 126°40.1′ W, BMT 256, 2,743

FIGURE 6.—*Munidopsis cascadia*, new species, male holotype, dorsal view.

m; OSUBI 00177, male, 51 mm CL, stn CP-1-E, 44°32.3′ N, 125°41.6′ W, OTB 77, 2,975 m; OSUBI 00178, gravid female, 37 mm CL, stn CP-1-E, 44°48.8′ N, 125°36.4′ W, BMT 287, 2,743 m; OSUBI 00179, male, 27 mm CL, stn CP-2-D, 44°53.7′ N, 126°33.4′ W, BMT 162, 2,884 m; OSUBI 00180, gravid female, 47 mm CL, stn CP-1-D, 44°55.4′ N, 125°40.6′ W, BMT 187, 2,760 m.

Comparative material.—*Munidopsis bermudezi* holotype, MCZ 10231, female, 38 mm CL, stn 2967, 19°43.5′ N, 74°57.5′ W, 2,434-3,020 m.

Diagnosis.—Moderate size (27-54 mm CL); carapace and legs densely covered with setae; stout eyespine on immovable eye stalk; two stout gastric spines; lateral margins of carapace smooth and slightly convex; resembles *Munidopsis bermudezi*.

Description.—Carapace length longer than wide, posterior width slightly greater than anterior width; strong antennal and anterolateral teeth separated by semicircular margin, a blunt tooth distal to anterolateral tooth, another blunt tooth at end of cervical groove; lateral margins raised

and slightly convex; pair of large, blunt, gastric spines, one pit behind each gastric spine, each pit surrounded by a small bare area; dorsal carapace surface densely covered with setae except for bare spots posterior to pits on gastric area, on cervical groove, and on anterior boundary of cardiac region; with setae removed dorsal surface fairly smooth except for rounded tubercles of posterior branchial area; one blunt ridge at unarmed posterior margin.

Rostrum 22% of carapace length, triangular in dorsal view, horizontal in lateral view, covered with setae, bluntly carinate dorsally.

Abdomen densely pubescent, unarmed; second, third, and fourth somites with two blunt transverse ridges.

Sternum with few setae and small tubercles; with transverse setose ridge opposite legs.

Eyestalks immovable; long, stout, pubescent internal eye spine much longer than diameter of the cornea.

Basal segment of antennular peduncle with one long spine midventrally, one long spine middorsally, and an inner toothed process.

Basal segment of antennal peduncle covered with setae, bearing outer ventral tooth and stout, inner, ventral spine. Second segment with large, outer, ventral spine and small, inner, ventral tooth.

Inner margin or merus of third maxilliped has three main spines, the posterior two have two points.

Cheliped shorter than carapace length; densely pubescent; epipods on chelipeds only; ischium with dorsal and ventral spine at meral articulation and a ventral row of six to seven small spines (including spine at meral articulation); merus with five spines at carpal articulation, dorsal row of six spines (including spine at carpal articulation), and two spines on the inner margin; carpus with four spines at chela articulation and one spine on inner dorsal surface; chela without spines.

Remarks.—Paratypes differ only slightly from holotype (Table 3). The chelipeds of four paratypes (USNM 134658, USNM 171339, OSUBI 00177, and OSUBI 00178) are relatively longer than those of the holotype and two other paratypes (OSUBI 00179 and OSUBI 00180), as shown by the ratio of carapace length to cheliped length in Table 3. In two specimens (OSUBI 00180 and USNM 134658), the lateral carapace margins posterior to the cervical groove have jagged edges instead of being smooth. The number of spines on the inner edge of the merus of the third maxilliped is constant except for one maxilliped of USNM 134658.

The number of spines on the cheliped segments is usually constant. Only the holotype has five spines at the carpal-meral articulation—the paratypes have four. There are four to five spines of the dorsal row on the merus; usually there are four on the paratypes. The number of spines on the ventral row of the ischium is variable, ranging from three to six. The dorsal inner spine on the carpus is always present, but is greatly reduced on paratype OSUBI 00179, and on OSUBI 00177 there are two spines.

A rhizocephalan parasite is present under the abdomen of USNM 171339.

Munidopsis cascadia was compared with the type of *M. bermudezi*. *Munidopsis cascadia* has stouter, blunter gastric spines, no spines on the lateral margin of the carapace, convex rather than a straight lateral margin of the carapace, and more pubescence.

Etymology.—*Munidopsis cascadia* is named from Cascadia Basin since all the specimens were found there.

Distribution.—Only seven specimens of *M. cascadia* are known, all from Cascadia Basin at 2,743-2,926 m. *Munidopsis bermudezi* has only been found in the Atlantic Ocean (Chace 1942;

TABLE 3.—Morphometry of *Munidopsis cascadia*.

Measurement (mm)	USNM [1]171338	USNM 134658	USNM 171339	OSUBI 00177	OSUBI 00178	OSUBI 00179	OSUBI 00180
Carapace length	54	45	38	51	37	27	47
Rostrum length	14	13	10	15	9	8	13
Anterior carapace width	36	21	18	23	17	12	23
Posterior carapace width	38	27	25	32	24	16	36
Cheliped length	43	41	33	49	35	22	37
Chela length	21	19	14	24	12	10	17
Carapace length/cheliped length	1.26	1.10	1.15	1.04	1.06	1.23	1.27

[1]Type-specimen.

Sivertson and Holthuis 1956; Pequegnat and Pequegnat 1970; Laird et al. 1976).

Munidopsis beringana Benedict 1902

Munidopsis beringana Benedict 1902:279 (original description), fig. 23.

Material.—USNM 134659, male 32 mm CL, male, 29 mm CL, female, 29 mm CL, stn Coos Bay #A, 43°17.3′ N, 125°49.3′ W, OTB 76, 3,000 m; OSUBI 00175, female, 31 mm CL, stn CP-2-E, 44°40.8′ N, 126°26.5′ W, OTB 48, 2,800 m; OSUBI 00176, male, 23 mm CL, stn CP-3-D, 44°53.5′ N, 127°27.5′ W, BMT 332, 2,826 m; 20 uncataloged specimens, no ovigerous females.

Remarks.—Three Oregon specimens (USNM 134659) were compared with Benedict's syntypes at the USNM by Henry B. Roberts.[2] He found considerable variation between the Oregon specimens and the syntypes regarding number of spines on the gastric area, length and spacing of the rugae on the carapace, and number of spines on the lateral edges of the carapace and on the meri of the chelipeds. The rugae of the Oregon specimens are, in general, shorter, more prominent, and more widely separated than the rugae of Benedict's specimens from the Bering Sea. The number of spines on the gastric area of the Oregon specimens varied from 4 to 17, on the lateral edge of the carapace from 2 to 4, and on the meri of the chelipeds from 7 to 12.

Distribution.—*Munidopsis beringana* was obtained in the deeper portions of Cascadia Basin from 2,800 to 3,041 m, on Tufts Plain from 3,354 to 3,990 m, and in the Bering Sea at *Albatross* stn 3603, 3,276 m (Benedict 1902).

Munidopsis tuftsi n. sp. (Figure 7)

Material.—Holotype, USNM 171336, male, 70 mm CL, stn TP-3, 44°40.8′ N, 133°26.3′ W, BMT 233, 3,717 m; Paratypes: USNM 171337, male, 36 mm CL, stn TP-4, 44°31.1′ N, 134°43.8′ W, OTB 334, 3,858 m; OSUBI 00181, male, 62 mm CL, stn TP-3, 44°39.8′ N, 133°37.2′ W, BMT 232, 3,724 m; OSUBI 00183, gravid female, 67 mm CL, stn TP-7, 44°58.0′ N, 133°14.5′ W, BMT 302, 3,500 m; OSUBI 01582, male, 15 mm CL, stn TP-6, 44°59.8′ N, 132°12.1′ W, BMT 302, 3,585 m.

Comparative material.—*Munidopsis crassa*: USNM 8563, female 45+ mm CL, *Albatross* stn 2224, 36°16.5′ N, 68°21′ W, 4,710 m; USNM 10803, female, 43 mm CL, *Albatross* stn 2573, 40°34.3′ N, 66°09′ W, 3,188 m; USNM 19289, male 44 mm CL, *Albatross* stn 2566, 37°23′ N, 68°08′ W, 4,795 m. *Munidopsis aculeata*: USNM 21277, male 39 mm CL, *Albatross* stn 3382, 6°21.0′ N, 80°41.0′ W, 3,281 m. *Munidopsis subsquamosa*: See *M. subsquamosa*.

Diagnosis.—Medium-sized species, 36-70 mm CL; triangular rostrum with small lateral spines; long eyespines; carapace wider posteriorly than anteriorly, covered with tubercles, first lateral spine not much larger than anterolateral spine; similar to *Munidopsis crassa*.

Description.—Rostrum triangular, bearing six (two right, four left) small spines laterally on distal half, upturned distally, dorsal median carina; dorsal surface with small tubercles; ventral surface smooth; length 26% of carapace length.

Carapace longer than wide, anterior width and length measured between first lateral spines less than posterior width; frontal margin bearing antennal spines, anterolateral spine on hepatic region with three spinules. First lateral spine on anterior lobe of branchial region with spinules on anterolateral spine. Several (five or six) small spines on lateral edge behind first lateral spine. Gastric area covered by crenulated tubercles bearing setae; six main spines—four at the base of the rostrum, two posterior to these—and numerous slightly smaller spines, smooth spaces between spines and tubercles. Cardiac and posterior branchial areas with crenulated transverse ridges bearing setae, smooth between ridges. Posterior margin unarmed, double ridge of small tubercles.

Sternum smooth, except for scattered setae on bumps and lateral ridges with many setae on top.

Abdomen spineless, covered with tubercles; ridges on somites two to four.

Ocular peduncle slightly moveable, extends beyond unpigmented cornea as stout inner spine, about twice the length of diameter of cornea, spinule on inner side of cornea.

Basal segment of antennular peduncle with one long slender spine midventrally; one long slender

[2]Henry B. Roberts, Senior Museum Specialist, U.S. National Museum, Washington, DC 20560, pers. commun. July 1970.

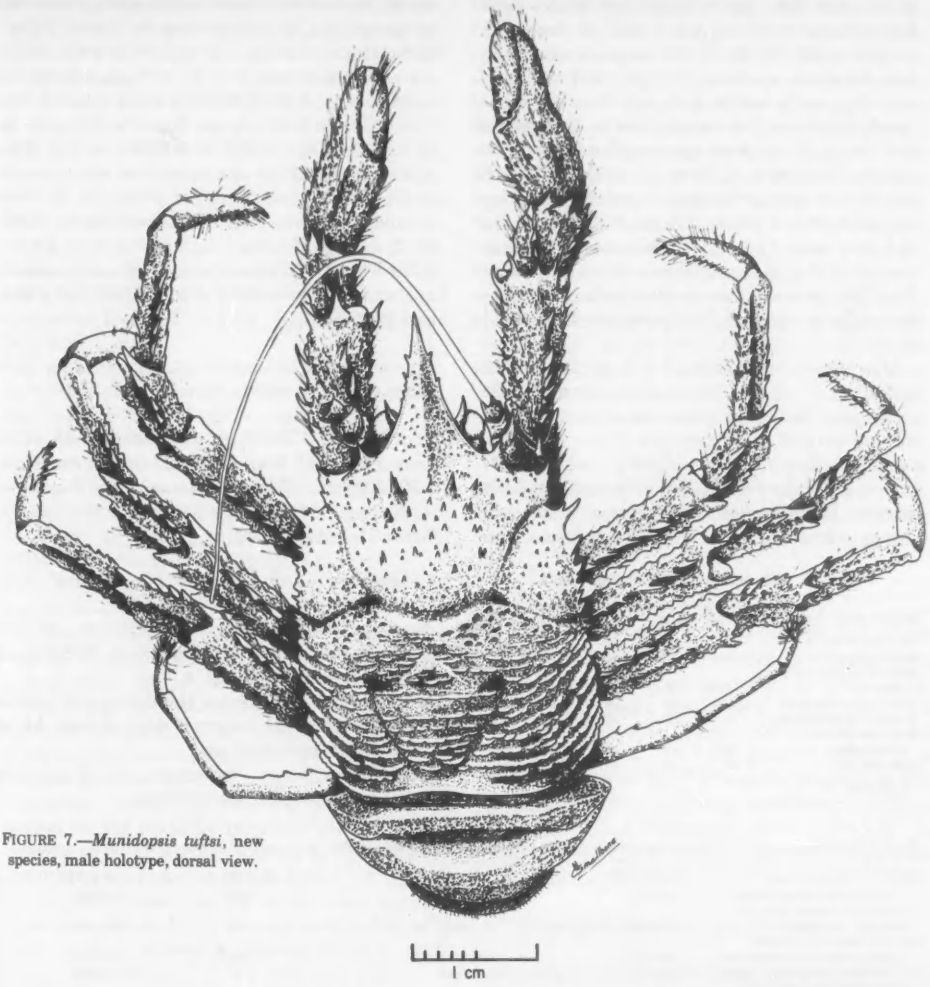

FIGURE 7.—*Munidopsis tuftsi*, new species, male holotype, dorsal view.

spine middorsally; a rounded, toothed process on inner side; and spinule on outer side.

Basal segment of antennal peduncle with two stout ventral spines. Second segment with outer spines and a small dorsal tooth. Third segment with four spines: inner, outer, and smaller dorsal and ventral spines. Fourth segment with two small, blunt, dorsal processes.

Inner margin of merus of third maxilliped with four main spines, plus several spinules.

Chelipeds with epipods. Chelipeds covered with setae and small tubercles, chela bears no major spines; carpus with five small spines at distal edge, and two rows of dorsal spines; merus with three to five small spines at distal edge, row of six to nine spines on dorsal surface, and two inner spines on left merus. Ambulatory legs without epipods, covered with setae and tubercles, and with spines on carina of propodus, carpus, and merus.

Remarks.—The three paratypes vary from the holotype in the number and presence of spinules

and spines. Both the holotype and OSUBI 00181 have spinules on the inner side of the ocular peduncle; OSUBI 00183 has no inner spinule but has an outer spinule; USNM 171337 has no spinules on the ocular peduncle. The number of small spines on the rostrum varies from two to seven with the smallest specimen having only two spines. Paratypes USNM 171337 and OSUBI 00183 have very few spinules on the anterolateral and first lateral spines compared with the other two specimens. The number of spines on the inner margin of the third maxilliped varies from two to four. The specimens are similar in the ornamentation of the carapace and in their proportions (Table 4).

Munidopsis tuftsi belongs to a species complex including *M. crassa*, *M. aculeata*, and *M. subsquamosa*. These species can be separated by observing several characteristics (Table 5). In this complex, *M. tuftsi* most closely resembles *M. crassa*, but differs in having a narrower anterior carapace and narrower width between first lateral spines compared with the posterior carapace width; anterolateral and first lateral spines of the same size; and small spines on the lateral edges of the rostrum. Although *M. tuftsi* has some characteristics in common with *M. aculeata* and *M. subsquamosa*, it has a distinctly more spinous ornamentation on the carapace. A very small specimen of *M. tuftsi*, OSUBI 01582, differs from the larger specimens only in the smoother carapace ornamentation and a larger ratio for anterior carapace width/posterior carapace width (Table 5). The ratio of cornea diameter divided by eyespine length is quite variable for *M. subsquqmosa*, but is usually between 0.46 and 0.55 for *M. crassa* and *M. tuftsi*.

Etymology.—*Munidopsis tuftsi* is named for Tufts Plain where all specimens were collected.

Distribution.—The four specimens of *M. tuftsi* were collected from Tufts Plain at depths of 3,500-3,858 m. *Munidopsis crassa*, the most similar species, has only been found from the Atlantic Ocean (Laird et al. 1976).

TABLE 4.—Morphometry of *Munidopsis tuftsi*.

Measurement (mm)	USNM [1]171336	OSUBI 00181	USNM 171337	OSUBI 00183	OSUBI 01582
Carapace length	70	62	36	[2]67	14.8
Rostrum length	18	17	9	[2]16	4.2
Rostrum length/carapace length	0.26	0.27	0.25	0.24	0.27
Anterior carapace width	30	29	18	32	7.6
Posterior carapace width	41	37	22	42	8.2
Width between first lateral spines	38	36	21	42	8.2
Right cheliped	84	69	43	76	14.1

[1]Holotype.
[2]Rostrum broken at tip.

Munidopsis subsquamosa Henderson 1885

Munidopsis subsquamosa Henderson 1885:414 (original description); Henderson 1888:152 (redescription), pl. 16, fig. 4.

Munidopsis subsquamosa Henderson var. *pallida* Alcock 1894:331 (original description); Alcock 1901:268 (redescription).

Munidopsis geyeri Pequegnat and Pequegnat 1970:149 (original description).

TABLE 5.—Morphometric ratios and spination that distinguishes *Munidopsis tuftsi*, *M. crassa*, *M. aculeata*, and *M. subsquamosa*.

Characteristics	*M. tuftsi*[1]	*M. crassa*[2]	*M. aculeata*[3]	*M. subsquamosa*[4]
1. Chela length/carapace length	0.41-0.44	0.42-0.45	0.65	0.37-0.46
2. Anterior carapace width/posterior carapace width	0.73-0.93	[5]0.90	0.92	0.80-0.98
3. Width between first lateral spines/posterior carapace width	0.93-1.00	1.03-1.13	1.05	1.07-1.25
4. Cornea length/eyespine length	0.48-0.55	0.36-0.49	0.89	0.52-0.82
5. First lateral spine compared with anterolateral spine	Same size	Larger	Same size	Larger
6. Armature on lateral edges of rostrum	Small spines	Minute teeth, none	None	Minute teeth and small spines
7. Rostrum turned up sharply	No	No	Yes	No
8. Number of spines on gastric area	2-6	2-4	6	2-12
9. Ornamentation on gastric area	Tubercles with blunt teeth	Tubercles with blunt teeth	Sparsely covered with small scalelike tubercles	Densely covered with large scalelike tubercles
10. Geographic distribution	Tufts Plain	Off North Carolina, SE of Martha's Vineyard, SE of Georges Bank	Gulf of Panama	Gulf of Panama, Cascadia Basin, Gulf of Mexico, Carribbean

[1]USNM 171336 (holotype), USNM 171337, OSUBI 00181, OSUBI 00183, OSUBI 01582.
[2]USNM 9563 (holotype; measurements from Smith (1885) because holotype is in poor condition), USNM 19289, USNM 10803.
[3]USNM 21277.
[4]USNM 21314 (holotype), USNM 171348, OSUBI 00185, OSUBI 00186, OSUBI 00187, *M. geyeri*—USNM 299042, TAMU 2-0574, TAMU 2-0575.
[5]Unknown for holotype.

Material.—Munidopsis subsquamosa: Holotype, USNM 21314, female 20 mm CL, *Albatross* stn 3361, 6°10.0′ N, 83°6.0′ W, 2,692 m; USNM 171348, male, 57 mm CL, stn Coos Bay #A, 43°17.3′ N, 125°49.3′ W, OTB 76, 3,000 m; OSUBI 00185, male, 70 mm CL, stn CP-3-C, 45°12.0′ N, 127°32.5′ W, BMT 324, 2,809 m; OSUBI 00186, female with parasite, 41 mm CL, stn NAD 20A, 44°30.1′ N, 125°24.3′ W, OTB 64, 2,772 m; OSUBI 00187, male, 23 mm CL, stn CP-1-E, 44°31.3′ N, 125°35.5′ W, OTB H-1, 2,736 m; OSUBI 00184, male with isopod parasite, stn CP-1-E, 44°40.5′ N, 125°40.0′ W, OTB 18, 2,850 m; 46 uncataloged specimens from off Oregon, smallest ovigerous female 54 mm CL.

Comparative material.—Munidopsis geyeri: Holotype, USNM 128812, male, 25 mm CL, *Alaminos* stn 69-A-11-92, 23°30′ N, 95° W, 2,928-3,001 m; TAMU 2-0574, female, 38 mm CL, male, 47 mm CL, *Alaminos* stn 70-A-10-48, 14°29.5′ N, 74°28.8′ W, 4,154 m; TAMU 2-0575, male, 46 mm CL, male, 18 mm CL, *Alaminos* stn 70-A-10-50, 15°50′ N, 77°24.5′ W, 2,654-2,791 m.

Remarks.—Munidopsis geyeri found in the Caribbean and Gulf of Mexico is here synonymized with *M. subsquamosa* from the Pacific and with *M. subsquamosa* var. *pallida* from the Indian Ocean. When compared with closely related species (*M. tuftsi, M. aculeata,* and *M. crassa*), *M. geyeri* and *M. subsquamosa* are identical (Table 5). *Munidopsis subsquamosa* and *M. aculeata* have similar carapace ornamentation, but with *M. subsquamosa* the scalelike tubercles are larger and closer together. The two species are also distinguished by characteristics 1, 3, 5, and 7 of Table 5. *Munidopsis crassa* and *M. tuftsi* have smaller, more spiny tubercles on the carapace and usually have longer, stouter eyespines than *M. subsquamosa*.

The distinctions given by Pequegnat and Pequegnat (1970) to distinguish *M. geyeri* from *M. subsquamosa*, and other taxonomic charcteristics were examined on the Oregon specimens of *M. subsquamosa*, the holotype of *M. subsquamosa*, and five specimens of *M. geyeri*, including the holotype. The range of variations of these characteristics for the Oregon specimens included those found for *M. geyeri*, except for the number of teeth on the lateral edges of the rostrum (Table 6). With the addition of the Oregon specimens, the maximum size and range of variation of *M. subsquamosa* is extended. Mayo (1974), who collected three specimens of *M. geyeri*, proposed that *M. geyeri* might become a synonym of *M. subsquamosa* when more material was available.

Alcock (1894, 1901) stated that *M. subsquamosa* var. *pallida* differs from *M. subsquamosa* by the former having only two spines on the gastric area of the carapace. Henderson (1885) did not state how many gastric spines the holotype has; I found only two.

Five of the Oregon female specimens have rhizocephalan parasites on the ventral side of the abdomen. Two other specimens had isopod parasites under the carapace on the posterior branchial area.

Distribution.—Munidopsis subsquamosa occurs mainly in the eastern part of Cascadia Basin from 1,829 to 3,000 m. This species is cosmopolitan, since it has also been collected at 3,431 m off Yokohama, Japan (Henderson 1888), 1,471 and 1,672 m off Panama (Faxon 1895), 3,299 m in the Bay of Bengal (Alcock 1894, 1901), 2,938-3,001 m in the southwest Gulf of Mexico (Pequegnat and Pequegnat 1970), 4,154 m in the Colombian Basin (Pequegnat and Pequegnat 1971), 2,790-2,650 m south of Jamaica (Pequegnat and Pequegnat 1971), and 3,111-3,496 m off Haiti (Mayo 1974).

Munidopsis verrucosus Khodkina 1973

Munidopsis verrucosus Khodkina 1973:1156-1159 (original description), fig. 1, 2.

Material.—Munidopsis verrucosus, USNM

TABLE 6.—Selected spine counts for *Munidopsis geyeri* and *M. subsquamosa*.

Characteristic	*M. geyeri* Type USNM 289042 (*n* = 1)	*M. geyeri* TAMU 2-0574 TAMU 2-0575 (*n* = 4)	*M. subsquamosa* Type USNM 21314 (*n* = 1)	*M. subsquamosa* Oregon specimens (*n* = 20) Mean	Range
Number of spines on 3d maxilliped (total, right + left)	9	8-10	6	7.8	6-11
Total number of teeth on lateral edges of rostrum	18	7-19	6	3.1	0-6
Number of spines on gastric area of carapace	2	[1]2	2	4.8	2-12
Number of spines behind anterolateral spine of carapace (total, right + left)	4	4-8	2	9.2	4-12

[1]Gastric area of carapace cracked on one specimen.

171347, gravid female, 25 mm CL, Gorda Ridge, 40°13.4′ N, 126°30.0′ W, OTB 104, 4,260 m; OSUBI 00172, female, 26 mm CL, stn TP-9, 45°01.1′ N, 135°12.6′ W, BMT 308, 3,932 m.

Remarks.—The Oregon specimens are indistinguishable from those described by Khodkina (1973). *Munidopsis verrucosus* is very similar to *M. granosa*, but differs in having an epipodite on the cheliped, setae on the tubercles of the carapace, plumose setae on portions of the chelipeds and pereiopods, no small antennal tooth, and no dorsal carina on the rostrum.

Distribution.—Khodkina (1973) collected three male specimens of *M. verrucosus* (33.8 mm, 34.8 mm, and 40.6 mm CL) from the Atakamsky Trench off Antofagasta, Chile, at two stations (lat. 23°47.1′ S, long. 71°03.2′ W, 4,300 m, and lat. 23°15.1′ S, long. 71°39.1′ W, 4,880 m). The two Oregon specimens were also found at great depths—3,932 m on Tufts Plain and 4,194 m on Gorda Ridge off northern California. Alcock (1901) collected one male specimen of *Munidopsis granosa* from 2,812 m in the Bay of Bengal.

Munidopsis latirostris (Henderson) Faxon 1895

Elasmonotus latifrons. Henderson 1885:416 (original description); Henderson 1888:160 (redescription), pl. 19, fig. 1.

Orophorhynchus latifrons. Milne-Edwards and Bouvier 1894:287 (in key to *Orophorhynchus*).

Munidopsis latirostris. Faxon 1895:81-82, 99 (changed name because genus synonomy caused prior usage of *M. latifrons*).

Material.—USNM 21285, female, 15 mm CL, *Albatross* stn 3381, 4°56.0′ N, 80°52.5′ W, 3,243 m; MCZ 4563, female, 16 mm CL, *Albatross* stn 3391, 7°15.0′ N, 79°36.0′ W, 280 m; USNM 171341, 14 specimens, stn CP-1-E, 44°28.2′ N, 125°32.3′ W, OTB 50, 2,800 m; OSUBI 00190, 28 specimens, stn CP-1-E, 44°35.7′ N, 125°34.3′ W, OTB 155, 2,830 m; OSUBI 00191, gravid female, 23 mm CL, male, 22 mm CL, male, 20 mm CL, stn C-P-3E Channel, 44°41.2′ N, 127°21.2′ W, BMT 407, 3,041 m; 541 uncataloged specimens from off Oregon, smallest ovigerous female 18 mm CL.

Remarks.—The characteristics of the Oregon specimens agree with those of the USNM and the MCZ specimens, but differ slightly from the type description (Henderson 1888). The "two slightly rounded elevations" at the base of the rostrum on the gastric area are blunt spines in the observed specimens. The "faint median carina" on the rostrum is a definite rounded ridge extending from the end of the rostrum to the blunt gastric spines (Figure 8).

The following observations are added to Henderson's description of *M. latirostris*. The basal segment of the antennular peduncle is swollen with two outer spines. The basal segment of the antennal peduncle has an outer tooth and an inner spine; the second segment has an outer stout tooth. The meri of the ambulatory legs have dorsal ridges with setae on the anterior side. Epipods are present on the chelipeds only.

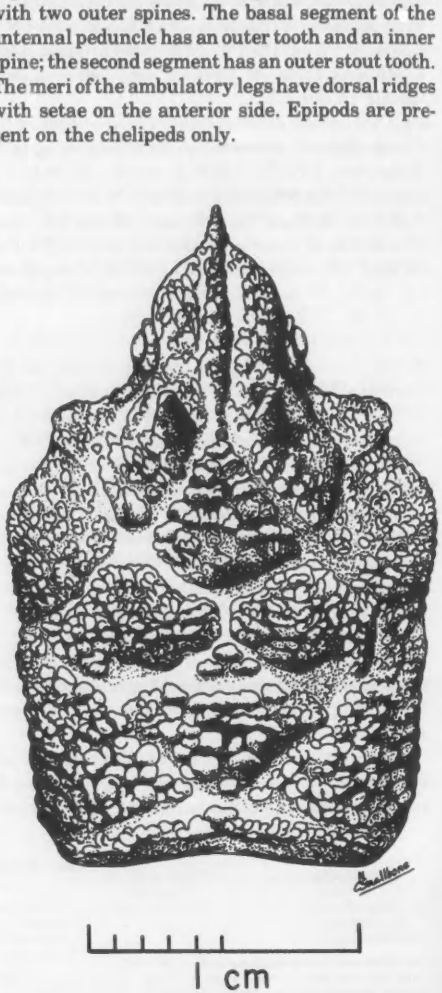

FIGURE 8.—*Munidopsis latirostris*, dorsal view of carapace.

In all specimens examined, the ocular peduncle extends beyond the eye as a blunt spine, although Benedict (1902) does not consider it an eyespine in his key. On the carina of the second, third, and fourth abdominal somites, there are slight median projections. Benedict (1902) considers these projections "armature on the abdomen confined to the median line."

The main variation of the Oregon and *Albatross* specimens is in the shape of the apex of the rostrum. Henderson (1888, plate XIX, figure 1) describes the rostrum as ending in an "acute apex," which is true for USNM 21285 and some of the Oregon specimens. In most of the Oregon specimens and MCZ 4563, the rostrum ends as a spine (Figure 9).

Rhizocephalan parasites occurred under the abdomen in 40 of 444 Oregon specimens; 23 hosts were females and 17 were males.

Distribution.—Munidopsis latirostris is the most abundant *Munidopsis* species found in Cascadia Basin, with a wide depth range, 1,900-3,021 m. This species has also been found in the tropical Pacific Ocean at 280 and 3,243 m off Panama (Faxon 1895) and at 1,958 m between Papua and Admiralty Islands (Henderson 1888).

VERTICAL AND GEOGRAPHIC DISTRIBUTION OF THE SPECIES

Twelve species of *Munidopsis* were captured in 51% or 146 of the total number of tows. Collections from both otter and beam trawls are included in the distributional analysis for more complete coverage. Although samples from otter trawls have been considered quantitative (number per hour trawled, Haedrich et al. 1975), beam trawls were designed to be more quantitative, giving number per square meter (Carey and Heyamoto 1972). Carney (1976) questioned the reliability of beam trawl data for area covered and expressed abundance as number per trawl for samples with similar wheel readings. In this paper, abundances are expressed as average number per trawl (number of specimens/number of trawls towed) because beam and otter trawls were towed for approximately the same time. Some specimens which can escape through 1.3 cm mesh liners are not sampled adequately. Adult densities of small species such as *M. ciliata, M. quadrata,* and *M. yaquinensis*, and immature individuals of the other species are probably underestimated. Immature specimens included *M. subsquamosa, M. latirostris, M. bairdii, M. tuftsi,* and *M. beringana*.

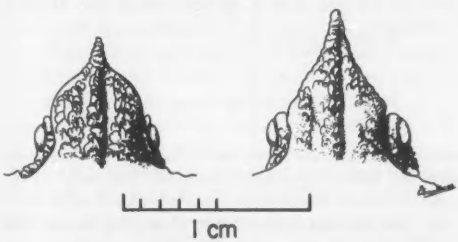

FIGURE 9.—*Munidopsis latirostris*, variation in rostrum, left rostrum ends as spine, right rostrum ends as acute apex.

Cascadia Basin off Oregon was probably the only area trawled adequately enough to sample all the species, since most species were collected at least several times there. The most abundant species, *M. latirostris*, contributed 73.0% of the total number of specimens. Three species together contributed 20.2% of the total: *M. bairdii* (7.5%), *M. ciliata* (6.2%), and *M. subsquamosa* (6.5%). These four species together represented 93.2% of all specimens, and were only found in Cascadia Basin. At the deepwater dumpsite stations in northern Cascadia Basin, all of the above except *M. ciliata* were collected. Five additional species (32 specimens) were also found on Cascadia Basin. Although 106 tows were taken on the continental slope off Oregon, only 5 tows yielded a total of three species (six specimens). Three species (17 specimens) were found on Tufts Plain (Table 7).

Abundances (number per trawl) for all *Munidopsis* species were about the same for the base of the continental slope (CP-1 line) and the CP-2 line (Table 7). However, the relative abundance of species changed from east to west. *Munidopsis latirostris* was the most abundant on both the CP-1 and CP-2 lines. On the CP-1 line, *M. subsquamosa* was second in rank, but on the CP-2 line, *M. subsquamosa* was fourth, *M. ciliata* was second, and *M. bairdii* was third (Table 7).

Eight of the 12 *Munidopsis* species were collected in Cascadia Basin, especially below 2,250 m (Figure 10). The single sample from Gorda Ridge, south of Cascadia Basin, contained one specimen of the rare, deepwater form, *M. verrucosus. Munidopsis quadrata* was the only species occurring over a wide depth range on the continental slope. A single tow on the lower part of the continental slope contained *Munidopsis* sp. and *M. subsquamosa*.

TABLE 7.—Occurrence of *Munidopsis* species on the continental slope, Cascadia Basin, and Tufts Plain (Figure 1).

Species	Total	Continental slope	Base of continental slope (CP-1, CP-x)	Cascadia Basin (CP-2)	Cascadia Basin (CP-3, CP-4)	Northern Cascadia (DWD)	Tufts Plain (TP-A, TP-B, TP-C)	Gorda Ridge
	number of specimens collected							
M. latirostris	586	0	362	132	77	15	0	0
M. bairdii	60	0	8	45	4	3	0	0
M. ciliata	50	0	2	48	0	0	0	0
M. subsquamosa	52	1	24	15	1	11	0	0
M. beringana	25	0	7	2	5	0	11	0
M. cascadia	7	0	4	3	0	0	0	0
M. yaquinensis	7	0	6	0	1	0	0	0
M. quadrata	6	4	0	0	0	2	0	0
M. tuftsi	5	0	0	0	0	0	5	0
M. aries	2	0	0	1	1	0	0	0
M. verrucosus	2	0	0	0	0	0	1	1
Munidopsis sp.	1	1	0	0	0	0	0	0
Total no. of *Munidopsis* spp.	803	6	413	246	89	31	17	1
Mean no./trawl	2.8	0.1	5.1	6.5	2.3	3.1	0.9	1.0
Total no. of trawls	289	106	81	38	38	10	18	1
Percent trawls with *Munidopsis* spp.	51	5	70	87	79	60	78	trace

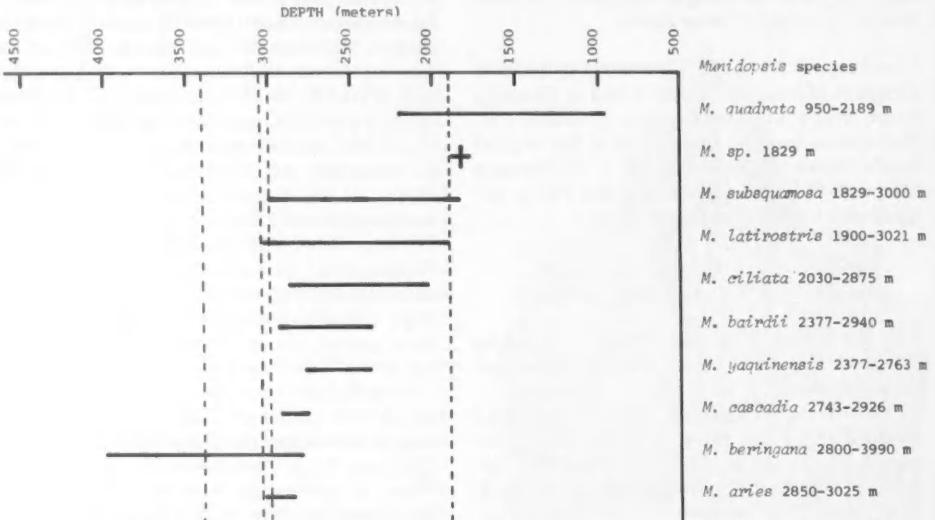

FIGURE 10.—Bathymetry of *Munidopsis* species from the continental slope, Cascadia Basin, and Tufts Plain off Oregon and Washington.

Four types of species distribution patterns emerge when all the stations on Cascadia Basin and Tufts Plain are considered (Figure 11). Two species, *M. latirostris* and *M. bairdii*, were found at most stations sampled in Cascadia Basin. The most abundant species, *M. latirostris*, was also the most widespread since it occurred at all but two of the Cascadia Basin stations. It occurred at

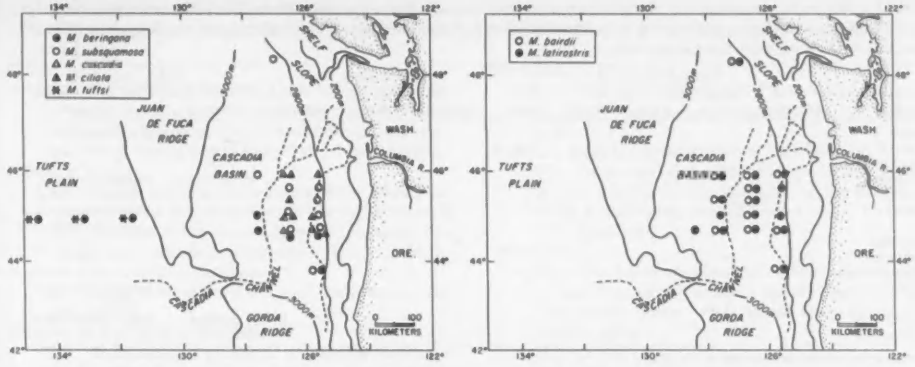

FIGURE 11.—Distribution of *Munidopsis* species off Oregon and Washington; upper—*M. cascadia, M. ciliata, M. tuftsi, M. subsquamosa,* and *M. beringana;* lower—*M. bairdii* and *M. latirostris.*

CP-4-E, the deepest and most western station on Cascadia Basin. Three species—*M. subsquamosa, M. cascadia,* and *M. ciliata*—occurred predominantly on the eastern side of Cascadia Basin. Only *M. beringana* was taken on both abyssal plains, notably occurring in Cascadia Basin only at the deeper, southern stations. Two species occurred only on Tufts Plain—*M. verrucosus* and *M. tuftsi.*

Carney (1976) found greater overlap in species distributions between Cascadia Basin and Tufts Plain for holothurians than for *Munidopsis* species. He described three basic distribution patterns: 1) present on Cascadia Basin but generally absent from the base of the continental slope, 2) present over all of Cascadia Basin extending to the eastern edge of Tufts Plain, and 3) present in the deepest and farthest offshore stations of Cascadia Basin and on Tufts Plain.

Two distributional studies of infauna on Cascadia Basin have shown great variation in species composition between different stations: Hancock's (1969) polychaete study along the CP-E line (Newport hydrographic line) and the gammarid amphipod study at stations CP-1-E and CP-3-E by Dickinson and Carey (1978). Carney (1976) showed that the species composition of polychaetes had greater variability between stations than that of the holothurians. Of the 20 most abundant gammarid amphipod species at the two Cascadia Basin stations, only 6 had similar abundances at both stations, and 10 species only occurred at one station (Dickinson and Carey 1978). Of the eight *Munidopsis* species I found on Cascadia Basin, only three occurred at both CP-1-E and CP-3-E. In all three groups (polychaetes, amphipods, galatheid crabs), there are differences in species composition between stations on either side of Cascadia Basin, which Dickinson and Carey (1978) suggested may be caused by decreasing sedimentation rates with increasing distance offshore, since other environmental conditions are constant across Cascadia Basin.

Of 65 known abyssal species of *Munidopsis*, Doflein and Balss (1913) found that a high percentage (71%) are endemic to specific oceanic regions. Since many abyssal species have been described from single or few specimens, the percentage of endemism declines with further collecting. My collections off Oregon extended the geographic range of seven species, three of which were previously known from only one location: *M. beringana* from the Bering Sea, *M. aries* from the Caribbean, and *M. verrucosus* from off Chile.

The number of cosmopolitan *Munidopsis* species, those found in all three major oceans, is small (Doflein and Balss 1913). Only one of the Oregon species, *M. subsquamosa,* can be considered cosmopolitan. Seven of the Oregon species are found only in the Pacific Ocean; one is also found in the Indian Ocean (Table 8). However, four of the Pacific and Indian-Pacific species have sibling species in the Atlantic Ocean, evidence that at one time the progenitors had broader distributions.

The four most abundant species from Cascadia Basin have tropical Pacific affinities (Table 8). Only one species, *M. beringana,* has arctic affinities and is found in the deepest parts of Cas-

TABLE 8.—Geographic occurrences of *Munidopsis* species from Cascadia Basin and Tufts Plain (Milne-Edwards 1880; Smith 1884, 1886; Henderson 1888; Faxon 1895; Alcock 1901; Benedict 1902; Rathbun 1904; Kensley 1968; Pequegnat and Pequegnat 1970, 1971; Khodkina 1973; Mayo 1974; Laird et al. 1976).

	Eastern Pacific Ocean					World ocean			Sibling species[1]	
Species	Endemic	North America	Arctic	Tropical	Bipolar	Pacific	Indian and Pacific	Atlantic	Species	Ocean
M. aries								+	—	—
M. bairdii				+				+	—	—
M. beringana			+			+			—	—
M. cascadia	+					+			*M. bermudezi*	Atlantic (Laird et al. 1976)
M. ciliata				+			+		*M. nitida*	Atlantic (Pequegnat and Pequegnat 1970)
M. latirostris				+		+			—	—
M. quadrata		+				+			—	—
M. subsquamosa				+			+	+	—	—
M. tuftsi	+					+			*M. crassa*	Atlantic (Laird et al. 1976)
M. verrucosus					+	+			*M. granosa*	Indian (Alcock 1901)
M. yaquinensis	+					+			—	—

[1]Most similar species, as described in this paper.

cadia Basin and on Tufts Plain. *Munidopsis verrucosus*, another deepwater species, may have a bipolar distribution since its only other known occurrence is in the Peru-Chile trench. The three new species may be endemic, but two of them have sibling species in the Atlantic Ocean. *Munidopsis quadrata* is only found off the west coast of North America from Washington to Mexico. Of the five species occurring off California and Mexico (Schmitt 1921; Haig 1956), *M. quadrata* is the only one whose range extends north to Oregon and Washington.

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USING MARKOV DECISION MODELS AND RELATED TECHNIQUES FOR PURPOSES OTHER THAN SIMPLE OPTIMIZATION: ANALYZING THE CONSEQUENCES OF POLICY ALTERNATIVES ON THE MANAGEMENT OF SALMON RUNS

ROY MENDELSSOHN[1]

ABSTRACT

The mathematics of Markov decision processes and related techniques are used to analyze a model relevant to salmon management. It is shown that the choice of grid can have a significant effect on the results obtained. Optimal policies that maximize total expected discounted return may be too variable. Smoothing costs are included to trade off long-run total return against the smoothness of the year-to-year fluctuations in the allowed harvest. Simpler, approximate policies that have a smoothing effect are also found. Preliminary analysis suggests the results are robust against misspecification of the parameters of the model. Concepts such as maximum sustainable yield would seem to impute a very high smoothing cost and are probably not practical for fish populations with a significant degree of randomness.

The history of most managed natural populations is one of sizable, nondeterministic variations in the dynamics of the population. This observed variation tends to have two sources: The first source is actual randomness in the system, such as that due to environmental variability, which will exist no matter how accurate our models become; and the second source is the inaccurate or incomplete specification of the transition probabilities themselves. Standard production models (Schaefer 1954; Pella and Tomlinson 1969; Fox 1970, 1971, 1975) assume deterministic dynamics, as do most recent bioeconomic analyses, as in Clark (1976) or Anderson (1977). For randomly varying populations, at best only extremely low harvests may be sustainable year to year, and it is not difficult to develop realistic scenarios where policies that are sustainable in a deterministic model would cause possible depletion in a stochastic model.

In this paper, the latest tools from stochastic optimization, particularly in the area of Markov decision problems (MDP's) are used to analyze a model relevant to salmon management. The viewpoint taken is that of the analyst, who must analyze trade offs and provide a decision maker with as few policies as possible that contain the maximum amount of information, rather than that of the decision maker, who ultimately decides if a particular concern or trade off is worthwhile. The salmon model is used as an example—the goal is to gain insight into managing randomly varying populations.

Ricker (1958) appears to be the first to examine the effects of variability on management. He used intuition and simulation to arrive at policies that are of the same general form as many of the policies to be discussed in this paper. However, Ricker presented no systematic way of developing optimal policies and made the incorrect assumption that the long-run stochastic behavior will have a mean equal to the deterministic equilibrium yield, with noise around this mean.

Reed (1974) derived qualitative properties of optimal policies if the random variable has a mean of 1, if it affects the population dynamics in a multiplicative manner, and if it has costs when the system is shut down (no harvesting) and then started up again (resumption of harvesting). Reed's results are not relevant to the model discussed in this paper, since he assumed the deterministic population model is concave, while the models examined in what follows are pseudoconcave. A more complete treatment of one dimensional stochastic growth models can be found in Mendelssohn and Sobel (in press).

Walters (1975) and Walters and Hilborn (1976, 1978) discussed a variety of topics as the concerns

[1]Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

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of this paper. Some of the techniques they discussed, particularly the filtering techniques (Walters and Hilborn 1978), are only appropriate if the model has an additive error term. While a Ricker spawner-recruit curve can be transformed to an additive model, many models do not have this feature.

I am presenting what I feel is an improved way to smooth out the fluctuations in the year-to-year harvests as compared with the method suggested in Walters (1975) and show that the Bayesian (adaptive) model discussed in Walters and Hilborn (1976) has an optimal policy with a very simple form that can be readily calculated.

Moreover, a rigorous approach is taken to define the model on a grid and the effects of the grid choice. None of the papers cited deal with this important question; new results are presented which show that the most serious effect of the grid is on the estimates of the long-run (ergodic) probabilities of the population dynamics when following a given policy. Particularly the tail properties of the ergodic distribution, i.e., the long-run probability of low harvest or low population sizes, are misestimated. This is a new finding even in the MDP literature, and has numerical implications, particularly when calculating the trade off between the mean harvest of a given policy and the long-run probability of undesirable events when following that policy.

THE MODEL

The models to be analyzed were developed by Mathews (1967) to describe the spawner-recruit relationships of sockeye salmon, *Oncorhynchus nerka*, populations in two rivers that run into Bristol Bay, Alaska. Oceanographic and other factors affect the number of recruits to a degree where the relationships can be modeled by the random equations:

Wood River:

$$x_{t+1} = \exp(d)\,(4.077 y_t)\exp(-0.800 y_t) \qquad d \approx N(0, 0.2098) \tag{1.1a}$$

Branch River:

$$x_{t+1} = \exp(d)\,(4.554 y_t)\exp(-1.845 y_t) \qquad d \approx N(0, 0.3352) \tag{1.1b}$$

where y_t is the number of spawners in period t, x_{t+1} is the (random) number of recruits in period $t+1$, and $d \approx N(a, b)$ denotes that d is a normally distributed random variable, with mean a and variance b.

For deterministic versions of Equation (1.1), the primary objective of management is MSY (maximum sustainable yield), which is equivalent to the largest per period growth of the deterministic model. The stochastic equivalent of this criterion is to maximize the average per period harvest, or gain optimality. Mathematically, letting E be the expectation operator, this is

$$\max \lim_{T \to \infty} \left[\frac{1}{T} E \sum_{t=1}^{T} (x_t - y_t) \right]. \tag{1.2a}$$

However, for many decision making situations, total expected discounted harvest may be a preferable criterion, since a discount factor can represent a measure of risk or uncertainty about the system, over and above the variability due to the random variable d. More formally, if α is a discount factor $0 \leq \alpha < 1$, the problem is to:

$$\text{maximize } E \left[\sum_{t=1}^{\infty} \alpha^{t-1} p(x_t - y_t) \right] \tag{1.2b}$$

subject to $0 \leq y_t \leq x_t$; and Equation (1.1)

where p is a weighting factor, which could be 1 or could represent the average weight of the salmon harvested.

All the results in this paper are for expected discounted return with $\alpha = 0.97$. For $\alpha = 1$, Equation (1.2a) must be used, since Equation (1.2b) is infinite for most policies. The choice of $\alpha = 0.97$ is arbitrary, though numerical runs for α ranging from 0.95 to 1.00 produced no significant changes in the results. When actually implementing a model, a careful choice of α must be made, and the sensitivity of the results to changes in the value of α should be tested. It should be mentioned that $\alpha = 1$ is just as much a discount factor as any other value and implies certain temporal preferences and attitudes towards risk that may not adequately reflect the decision maker's preferences.

The shortcomings of Equation (1.1a) or (1.1b) should also be noted, such as no account is taken of ocean harvesting of the salmon, particularly by a foreign nation. This just reinforces the idea that the purpose of this analysis is not optimization per

se, but rather to provide the decision maker with added insight and reasonable first choices.

Defining the Model on a Discrete Grid

In order to make Equation (1.2) amenable to numerical methods, it is necessary to define both the state space and the action space on a discrete grid, and then to redefine the transition probabilities, etc., on this grid. Several authors (Fox 1973; Bertsekas 1976; Hinderer 1978; Waldmann 1978; Whitt 1978; Larraneta[2]) have suggested techniques to reduce MDP's to a grid and give bounds on the error due to the approximation. I have shown elsewhere (Mendelssohn[3]) that grid choice can have a significant effect on the analysis. An optimal policy and the value of an optimal policy may not be greatly affected by the choice of grid, but the estimated probabilistic behavior of the population dynamics is affected significantly by the choice of grid.

A first effort then is to find an adequate grid for the problem, a grid fine enough for both the desired accuracy and for realistic approximations of observed population sizes and coarse enough for computational efficiency. Increased computational efficiency makes it reasonable to solve many variations of a given model, which allows for a more thorough exploration of the management questions of interest and their sensitivity to key assumptions.

Several different grids were tried for Equation (1.2) for both the Branch and Wood Rivers.

To define Equation (1.2) on a given grid, suppose a grid of k points has been chosen on which to discretize the problem and assume, as is reasonable for this problem, that the reduced action space (how many spawners to leave) is equivalent to the state space (how many recruits are observed at the beginning of the period). From Equation (1.1), letting R_1 and R_2 represent the parameters of the Ricker equation

$$P(x_{t+1} \leqslant \omega | y_t) = P[(e^d) R_1 y_t \exp(-R_2 y_t) \leqslant \omega]$$

$$= P(d \leqslant \ln\omega - \ln a) \qquad (2.1)$$

where $a = [R_1 y_t \exp(-R_2 y_t)]$. Let Φ be the standard normal integral for a random variable $\bar{d} = d/\sigma$, and let x_i, x_{i+1} be any two adjacent points on the grid. Then:

$$P(d \leqslant \ln x_i - \ln a) = \Phi\left(\frac{\ln x_i - \ln a}{\sigma}\right)$$

$$P(d \leqslant \ln x_{i+1} - \ln a) = \Phi\left(\frac{\ln x_{i+1} - \ln a}{\sigma}\right)$$

so that one method of defining the transition probabilities on a grid is:

$$P(x_{t+1} = x_{i+1} \mid y_t) = \Phi\left(\frac{\ln x_{i+1} - \ln a}{\sigma}\right) - \Phi\left(\frac{\ln x_i - \ln a}{\sigma}\right).$$

The discrete probability when the action is y_t is equal to the total probability of going to any state in the interval (x_i, x_{i+1}).

If zero is included as a state, the procedure needs to be modified slightly. Suppose the probability of going to x_1 is known for each decision y. Then an arbitrary fraction of this probability is assigned as going to the zero state. In this paper, one-half of the probability in the interval $(0, x_1)$ is assigned to the zero state. The results have been found not to be sensitive to the value of the fraction; this is because zero is an absorbing state. Either there exists a policy that never reaches $(0, x_1)$ and hence never reaches zero, or else with probability one the population goes to zero in finite time. Hence, it is the size of $(0, x_1)$ that most influences the results, not the fraction of this total that is assigned to going to the absorbing state.

Adding an absorbing state is sensible if the absorbing state is thought of as all states at low enough population levels such that it would take years for the fishery to recover again, if it recovers at all. Without the absorbing state, the models in Equation (1.1a, b) will always recover in fairly short order. Since fisheries can be depleted, the

[2]Larraneta, J. C. 1978. Approaches to approximate Markov decision processes. Paper presented at Joint National ORSA/TIMS Meeting, Nov. 13-15, 1978, Los Ang., Calif.

[3]Mendelssohn, R. 1978. The effects of grid size and approximation techniques on the solutions of Markov decision problems. SWFC Admin. Rep. 20H, 15 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv. NOAA, Honolulu, HI 96812.

inclusion of an absorbing state would seem to be a more realistic assumption. It is included in what follows.

A coarser grid implies, in a sense, less information about the state of the system. As the interval $(0, x_1)$ becomes large, our information has decreased about the true state of the population and this increased uncertainty is reflected in increased risk of absorbtion. Similarly, a finer grid implies more exact information—a grid should not be used which is finer than the precision of the estimate of the population size.

Optimal policies for grids of 16, 26, 51, 101, and 501 equally spaced points (including zero) for both rivers are shown in Table 1. The optimal equilibrium population for the equivalent deterministic models are shown also. All numbers are in units of millions of fish.

The optimal policies are all of the base stock variety, i.e. it is optimal to harvest to a fixed number of spawners, or else not to harvest at all. If the 501-point grid is taken as the standard, it can be seen that each coarser grid has as its base stock size the grid point closest to the base stock size for the 501-point grid.

Figure 1 gives the long-run (ergodic) cumulative distribution of being in any state when following an optimal policy on grids of 16, 26, 51, and 101 points. Grid size can be seen to play a crucial part in estimating the probabilistic behavior of the population. For the Wood River, extinction with probability one is predicted on grids of 16 and 26 points, while the probability is zero on grids of 51 and 101 points, so long as zero is not the initial state. Similar but not identical results are valid for the Branch River. It should be emphasized that for $\alpha = 1$, i.e., when the objective is given by Equation (1.2a), the estimated average per period harvest of any policy depends entirely on the ergodic distribution that arises from that policy. Therefore, this variation in estimated long-run behavior due to changes in grid size is nontrivial.

Probability one of extinction occurs because for a finite state, irreducible Markov chain with an absorbing state, the absorbing state is reached in finite time with probability one. However, for the larger grids, there exist policies that are reducible, in the sense that if the chain does not start in the interval $(0, x_1)$, it will never enter that interval. Since $P[x_t \epsilon (0, x_1)] = 0$, and a fraction of this probability has been assigned to the zero state, then $P(x_t = 0) = 0$. When using the smaller grids that induce Markov chains that are irreducible, the estimated time till absorption varies greatly also. For example, for the Branch River, if $P(x_1 = 0) = 0$ and $P(x_1 = \omega) = 1/(N-1)$, where ω is a grid point and N is the number of states, then a 16-point grid predicts absorption with probability one after 2,000 iterations, the 26-point grid predicts only a 76% chance of absorbtion after 2,000 iterations, and the 51-point grid predicts only a 17% chance of absorption.

When maximizing total expected discounted return, the discounted mean return depends on the values of these intermediate probability distributions, so that coarser grids can be expected to underestimate the long-run value of the harvest.

Finally, for the Wood River, note that the 51- and 101-point grids have similar long-run behavior. These results suggest that in order to find

TABLE 1.—Optimal policies for the different grid sizes.

Wood River	Grid size	Branch River
$y_t = \min(x_t, 0.9333)$	16	$y_t = \min(x_t, 0.3333)$
$y_t = \min(x_t, 0.840)$	26	$y_t = \min(x_t, 0.4000)$
$y_t = \min(x_t, 0.700)$	51	$y_t = \min(x_t, 0.3000)$
$y_t = \min(x_t, 0.770)$	101	$y_t = \min(x_t, 0.3500)$
$y_t = \min(x_t, 0.742)$	501	$y_t = \min(x_t, 0.3500)$
Equilibrium stock 0.735	Deterministic	Equilibrium stock 0.345

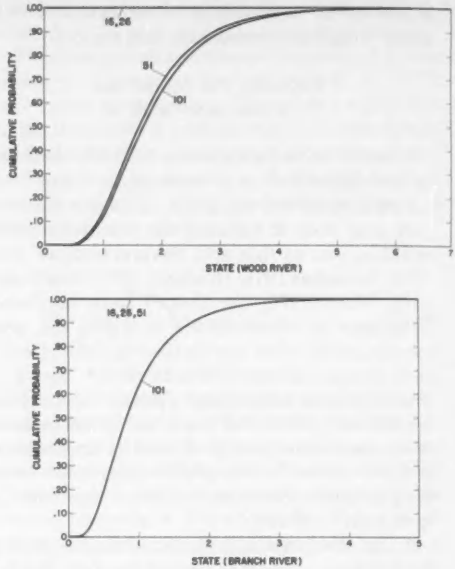

FIGURE 1.—Ergodic cumulative distributions for optimal harvesting strategies on grid sizes of 16, 26, 51, and 101 points for the Wood River and the Branch River.

good policies, it is only necessary to use a grid size of 26 to 51 points for the problems under consideration. However, to analyze the long-run (probabilistic) behavior of a given policy, it is necessary to use a grid containing no fewer than 100 points.

It should be reemphasized that the reason for considering a coarser grid is that a smaller problem size allows for many problems to be solved at a small cost. This is desirable to obtain insight into the sensitivity of the problem. However, it is possible to solve quite large problems, making use of a variety of methods to accelerate computations (see for example Porteus 1971; Hastings and van Nunen 1977). For example, the 501-point grid for the Branch River used 1.80 s of CPU (central processing unit) time to perform the optimization. Computations, when smoothing costs are included (see Policy Analysis section), have 2,601 states. These used about 5 to 6 min of CPU time to perform the computations, but at a cost of about $20. Our experience is that it is possible to obtain reasonable estimates using coarse grids and that this suffices for initial policy investigation. However, it is worthwhile to reanalyze the final two or three problems of greatest interest on a finer grid.

POLICY ANALYSIS

For the Wood River, the optimal policy for Equation (1.2) is given by

$$y_t = \text{minimum}\,(0.770, x_t)$$

and it produces a mean per period harvest of 1.14758, and a standard deviation in the harvest of 0.8963. The median harvest is 0.91, and no harvest occurs roughly 4.3% of the time. A harvest of 25% or less of the mean harvest occurs roughly 15% of the time, while a harvest greater than the mean harvest occurs approximately 38% of the time.

Similarly, for the Branch River, an optimal policy for Equation (1.2) is given by

$$y_t = \text{minimum}\,(0.300, x_t)$$

and it produces a mean per period harvest of 0.6622, and a standard deviation in the harvest of 0.6120. The median harvest is roughly 0.500; there is a 3.9% chance of no harvest. A harvest of 25% of the mean harvest or less occurs roughly 14.5% of the time, and a harvest greater than the mean harvest occurs approximately 61% of the time.

While these policies are similar in form to policies that are optimal for a deterministic version of Equation (1.2), they differ greatly in the year-to-year dynamics. There are two ways of finding the optimal deterministic policy. The first way is to assume a general model of the form:

$$x_{t+1} = R_1 y_t \exp(-R_2 y_t)$$

The second method is to assume a general model of the form:

$$x_{t+1} = E \exp(d) R_1 y_t \exp(-R_2 y_t)$$

where as before, R_1 and R_2 are the parameters of the Ricker equation. The second method is preferable since it uses all the information available. As d is a normal random variable with mean zero and variance σ^2, it is easy to show that $\exp(d)$ is a lognormal random variable with expectation $\exp(\frac{1}{2}\sigma^2)$. Solving for the optimum sustained yield (OSY) population size for each river gives:

	Wood River	*Branch River*
x_{OSY}	0.735	0.345
OSY	1.11346	0.63804

Both OSY values are lower than the mean per period harvests in the stochastic models, but the variation is too high to allow this amount to be harvested each year. However, the x_{OSY} level is a good estimate of the base stock size, and it is known a priori from Mendelssohn and Sobel (in press) that a base stock policy is optimal.

In the deterministic model, once x_{OSY} is reached, both the population size and the harvest size are maintained at steady, equilibrium levels. An optimal policy for the stochastic model, however, produces large fluctuations in both and may allow no harvesting 1 yr out of 25 in the long run. For many fisheries, these "boom and bust" conditions may not be acceptable. Many people, especially those with interest or mortgage payments, as are many fishermen, are concerned about smoothness of income received as well as the total amount received. The final decision on the acceptable amount of fluctuation is, of course, up to the decision maker with appropriate input.

There are several methods available to try to find a balance between the smoothness of the random income stream and its total discounted expected value. Walters (1975) and Walters and Hilborn (1978) suggested fixing a given mean harvest

u, and then finding a policy that minimizes $\lim_{T\to\infty} E\frac{1}{T}\sum_{t=1}^{T}(z_t-u)^2$. This methodology depends on the values of u chosen. It also determines the policy that minimizes the approximate long-run variance for a given long-run mean harvest. This is not equivalent to reducing the size of the year-to-year fluctuations.

A second method is to include "smoothing costs" into the one-period return. This approach has been studied analytically by Mendelssohn.[4] Let γ be the cost of a unit decrease in the harvest from year to year, and let ϵ be the cost of a unit increase in the harvest from year to year.

If z was harvested last year, then net revenues this year, for any harvest z_t, are decreased by

$$\begin{cases} \gamma(z-z_t) & \text{if } z>z_t \\ 0 & z=z_t \\ \epsilon(z_t-z) & z<z_t \end{cases}.$$

Amended to Equation (1.2), this would imply a one-period net benefit of

$$p(x_t - y_t) - \gamma[z - (x_t - y_t)]^+ - \epsilon[(x_t - y_t) - z]^+$$

where $(a)^+$ denotes the positive part of a. An alternate form is to let $e = (\gamma-\epsilon)/2$ and $c = (\gamma+\epsilon)/2$. Then the one-period return is:

$$p(x_t - y_t) + e(x_t - y_t) - c\,|\,(x_t - y_t) - z\,| - ez.$$

One advantage to the smoothing cost approach over other approaches is that p, e, and c can be normalized so as to be interpreted as relative prices. That is, the normalized values $p = 1$, e/p, and c/p can be interpreted as the value of having the between period harvest "smoothed" by one unit relative to the value of one unit of additional harvest. Actual relative values are often difficult to determine. But by parameterizing on e and c, it is possible to present a decision maker not only a range of possible "optimal" policies and their consequences, but also some feeling for the relative trade off between total income and the smoothness of the received income stream.

For the Wood and Branch Rivers, two sets of computations were performed. The first set assumes that $\gamma = \epsilon$, i.e., there is an equal concern for increases in allowable harvest as well as for decreases. This is equivalent to $e = 0.0$ and $c = \gamma$ (or equivalently ϵ). The motivation for this cost structure is that fishermen typically resist any decrease in the allowed harvest, hence $\gamma>0$. However, allowing increases in the harvest size often signals fishermen to gear up and invest in equipment, thereby making it even more difficult to decrease the allowable harvest later on. Therefore this cost should be equal to a cost due to a decrease in the harvest.

As a counterbalance to this, a second set of computations were performed with $\gamma>0$ but $\epsilon = 0$, i.e., a cost only if the harvest is decreased. This is equivalent to $c = e = \gamma/2$.

For the first set of computations, with $e = 0.0$ and $p = 1.0$, values of c of 0.25, 0.50, 0.75, 1.00, 1.25, 1.50, 1.75, and 2.00 were used. These are equivalent to relative values of ⅛, ¼, ⅜, ½, ⅝, ¾, ⅞, and 1. For the second set of runs, with $c = e$, and $p = 1.0$, values of 0.25, 0.50, 0.75, 1.00 and 1.25 were used. These are equivalent to a ratio of γ/p equal to ¼, ½, ¾, 1, 1¼. The results are summarized in Figure 2(a)-(m) and Figure 3(a)-(m), which show an optimal policy for each river for each of these cases. All computations were performed on 26-point grids.

The figures are read as follows. Suppose z was harvested last year and x is the observed population size this period. Find the point (x, z) on the graph and follow the arrow in that zone to the appropriate boundary as indicated. Then read off the z value of this point; this is the optimal amount to harvest during this period.

For example, if $c = 0.50, e = 0.00, x_t = 0.84$, and the harvest last period was 0.28, Figure 2(b) shows that the optimal policy for the Wood River is to harvest 0.28 this period. Note that the dashed line is the equivalent base stock harvest with no smoothing costs.

While the policies in Figures 2 and 3 are optimal for the given relative values of p, e, and c, they are complex in nature and would be difficult for a layperson to understand. Practical management often implies determining simpler, good but suboptimal policies that achieve the same objectives. These policies are often more desirable since they

[4]Mendelssohn, R. 1976. Harvesting with smoothing costs. SWFC Admin. Rep. 9H, 26 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.

are easier to implement and easier to explain the rationale to the public.

As an example of suboptimal, approximate policies, the following nine modified base stock policies were examined:

Wood River

1) Base stock policy, base stock size = 0.84.
2) Policy of base stock size of 0.56 till 2.52, then a base stock size of 0.84.
3) Policy of base stock size of 0.56 till 1.40, then a base stock size of 0.84.
4) Harvest 0 till 0.28, harvest 0.28 till 0.84, a base stock size of 0.56 till 2.52, then a base stock size of 0.84.

Branch River

5) Base stock policy, base stock size of 0.40.
6) Base stock size of 0.4 till 1.6, then a base stock size of 0.6.

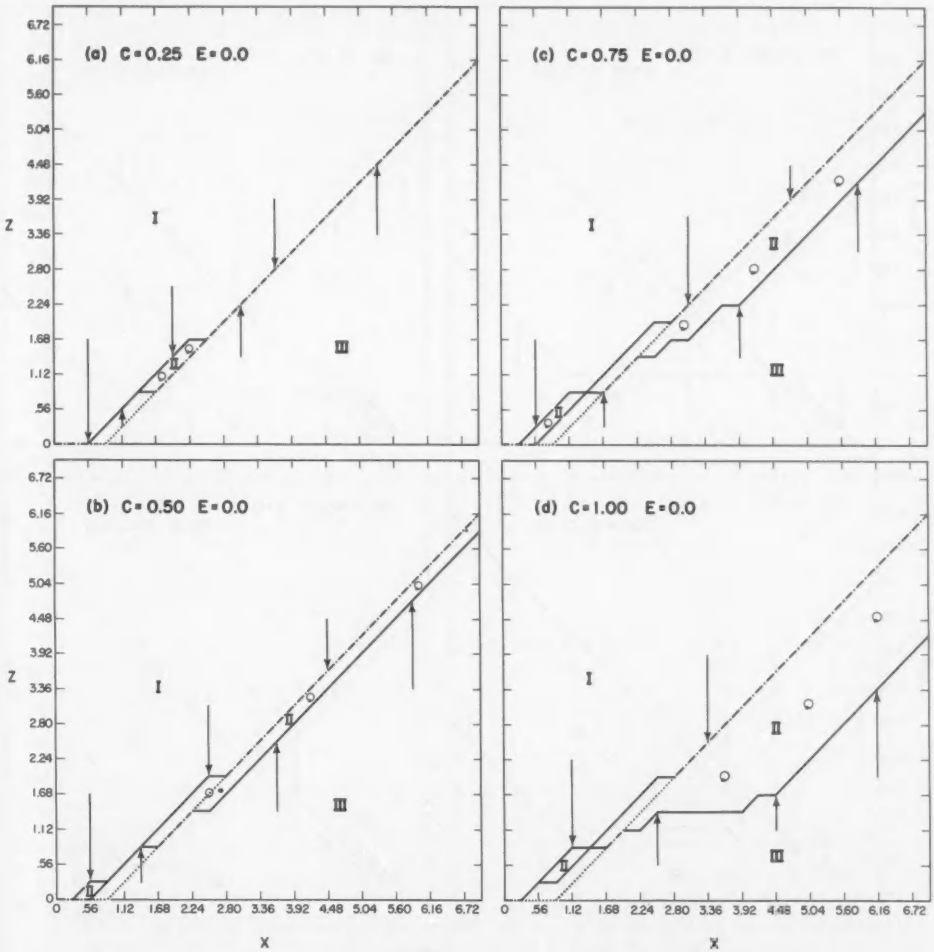

FIGURE 2(a-m).—Optimal policy functions for the Wood River for various assumptions about the relative value of smoothing costs. (See text for details).

7) Base stock size of 0.2 till 0.6, then a base stock size of 0.4.
8) Base stock size of 0.2 till 1.0, then a base stock size of 0.4.
9) Base stock size of 0.2 till 0.4, base stock size of 0.4 till 1.2, base stock size of 0.6 after that.

These nine approximate policies were devised by examining the functions that define the three regions in Figures 2 and 3. These approximate the boundaries of the three regions where the smoothing costs are one-fourth to one-half the per unit value of the harvest. The mean per period harvest, variance, standard deviation, median per period harvest, etc. for these nine policies are given in Table 2.

Policies 3 and 4 for the Wood River and 8 and 9 for the Branch River demonstrate how these approximate policies tend toward smoothing policies. For example, policy 4 has the same median harvest as the optimal base stock harvest, almost never closes the fishery, significantly de-

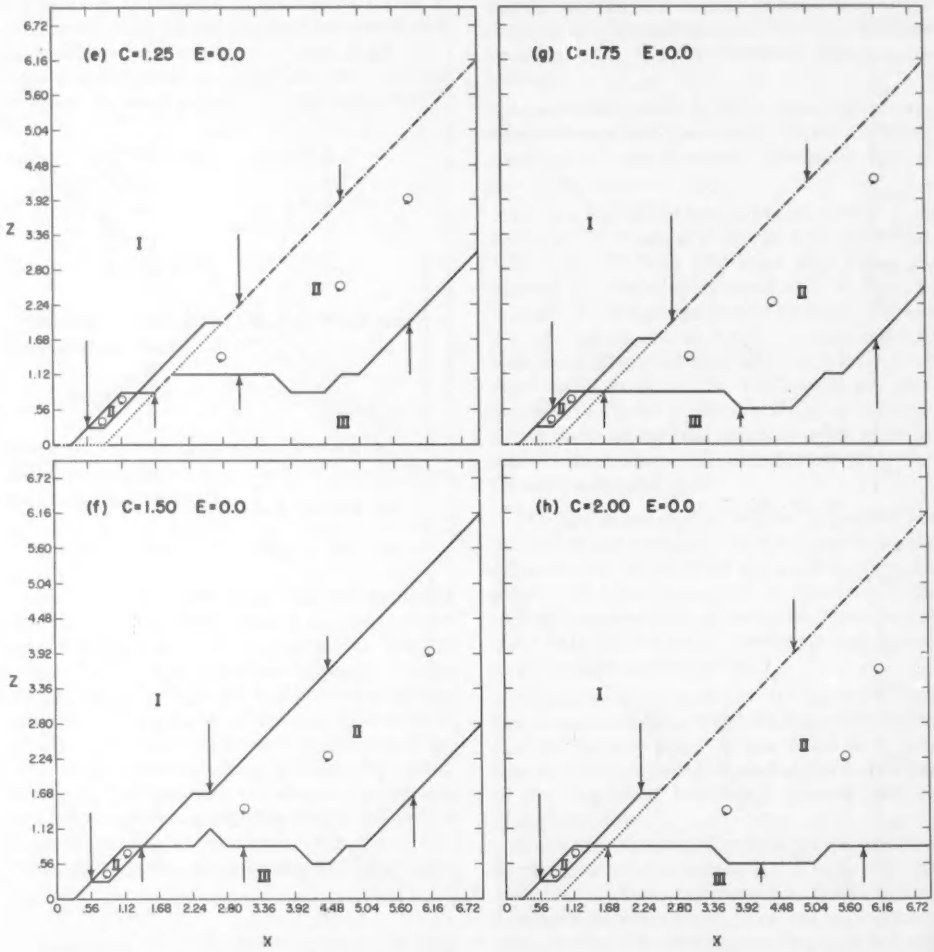

FIGURE 2.—Continued.

creases the percent of time there are low catches, and only reduces the mean per period harvest by 33,800 fish. In order to achieve a smoother catch, "potlatch" harvests from time to time have been sacrificed.

When looked at closely, these policies are actually very intuitive and represent an interesting variant of a base stock policy. These policies replace a single base stock size by a dual base stock size policy. The first base stock size is lower than the original one, while the second base stock size is greater than or equal to the original base stock size. This means that there are fewer states where there is no harvesting, but also lowers the likelihood of the really big harvests. The mean per period harvest tends to be very sensitive to these big harvests, while the median is not, particularly since the very large harvests are not too frequent.

It is curious that the population dynamics are so sensitive to such fine tuning, for the difference between policy 1 and policy 3, say, is quite marginal. It would be an interesting area of future

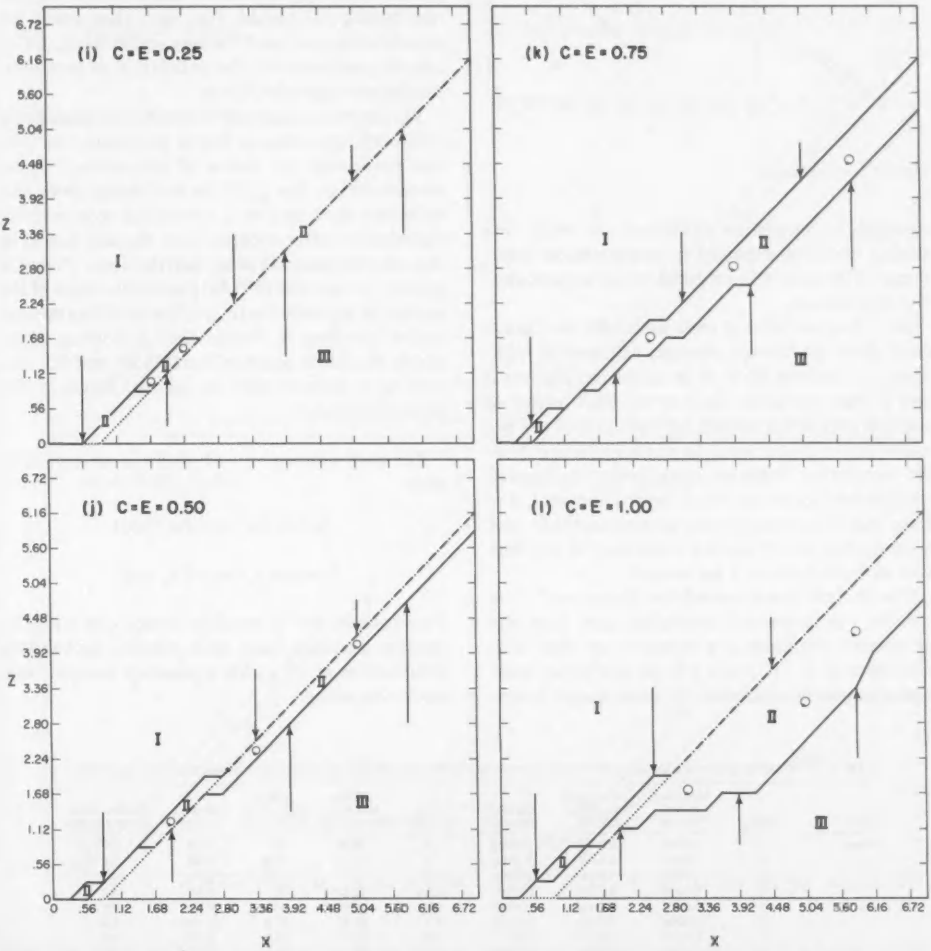

FIGURE 2.—Continued.

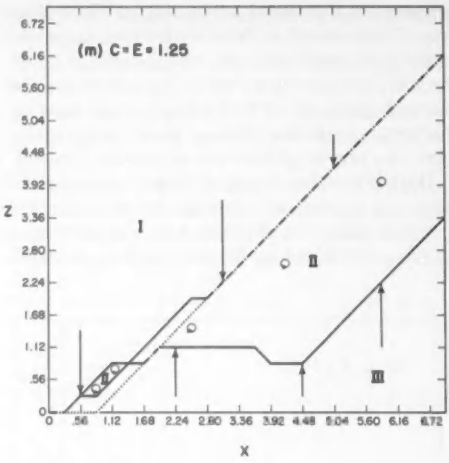

FIGURE 2.—Continued.

research to determine guidelines for when fine tuning would be expected to produce such "trimming" of the tails of the ergodic (long-run probability) distribution.

Including smoothing costs also tells us a great deal about traditional concepts of fisheries management, such as MSY. It is clear from Figures 2 and 3 that anything close to an MSY policy is optimal only if the smoothing costs exceed the per unit value of the harvest. As whole systems of laws for regulating fisheries have been constructed around the idea of smooth, constant harvests, it is clear that this imputes lower average catches, and a significant preference for constancy of the harvest over total amount harvested.

The analysis has assumed that Equation (1.1) or similar equations are available, and that the parameter estimates are accurate (in this case, estimates of R_1, R_2, and σ^2). In the latter case, management measures would seem more reasonable if they were known to be robust against misspecifying the parameters. This involves knowing how an optimal policy and total expected value would vary if the true underlying parameter values differ from those specified, and also how the estimate of the long-run probability distribution differs from the true one.

Walters and Hilborn (1976) have examined a similar question of trying to solve the Bayes model of this problem, i.e., where there is an original prior probability given to each value of the parameter, and this probability is updated each period using Bayes theorem and the observed values during the period. However, they could not obtain a solution, and Walters and Hilborn (1978) raised questions as to the validity of some of their numerical approximations.

Fortunately, qualitative results are possible for this particular class of Bayes problems. Let Θ be the parameter (or vector of parameters) under consideration. Let $q_0(\Theta)$ be the initial prior distribution on Θ, and let $q_n(\Theta)$ be the updated prior distribution after n period has elapsed. Let Ω be the set of all possible prior distributions. Then it is proven in van Hee (1977a) that if the state of the system is expanded to (x_t, q_t), the resulting optimization problem is Markovian. Following arguments similar to those in Scarf (1959) and van Hee (1977a) it follows that an optimal Bayes policy takes the form:

For each element $q \in \Omega$, there is an $x(q)$ such that:

$$\text{do not harvest if } x_t \leq x(q)$$

$$\text{harvest } x_t - x(q) \text{ if } x_t > x(q).$$

For example, if σ^2 in the distribution of d is itself a random variable, then each possible probability distribution of σ^2 yields a possibly unique base stock size policy.

TABLE 2.—Vital statistics for the nine policies approximating the smoothing cost policies for Wood and Branch Rivers.

River	Policy	Mean per period harvest	Variance of per period harvest	Standard deviation	% time no catch	% time less than 25% of mean	% time greater than mean catch	Median catch	Relative value: smoothing/price
Wood	1	1.1357	0.8468	0.9202	5.6	16.8	39	0.98	0/1
	2	1.0993	0.5460	0.7389	1.7	10.7	39.8	0.98	1/8
	3	1.1203	0.6506	0.8066	1.1	7.7	43.2	0.91	1/4
	4	1.1019	0.5758	0.7588	0.02	10.47	40	0.98	1/2
Branch	5	0.6528	0.3982	0.6310	9.2	21.8	40	0.500	0/1
	6	0.6290	02532	0.5032	9.1	21.5	37.2	0.500	1/4
	7	0.6272	0.3077	0.5547	1.2	27.7	31.3	0.400	1/2
	8	0.5920	0.2202	0.4693	1.9	35.7	26.3	0.500	3/8
	9	0.5995	0.3038	0.5512	0.72	22.83	39.3	0.500	3/4

Van Hee (1977a) defined a set of policies that he terms Bayes equivalent policies. For problems such as the salmon models under discussion, a Bayes equivalent policy would be found as follows:

1) At the start of the period, the prior probability distribution is $q(\Theta)$.

2) The expected transition function (expectation with respect to Θ) is calculated, i.e.,

$$p(d, q) = \int p(d \mid \Theta) q(d\Theta) \qquad (4.1)$$

where $p(\cdot \mid \cdot)$ describes the dependence of the random variable d on Θ.

3) $p(d, q)$ is used to solve a non-Bayesian Markov decision process, with $p(d, q)$ as the transition function.

4) The optimal policy from step 3 above is used for one period.

5) $q(\Theta)$ is updated using Bayes theorem and the observations from the last period, and the updated $q(\cdot)$ is used in step 1 at the next time period.

It is worth noting that a Bayes eqivalent policy

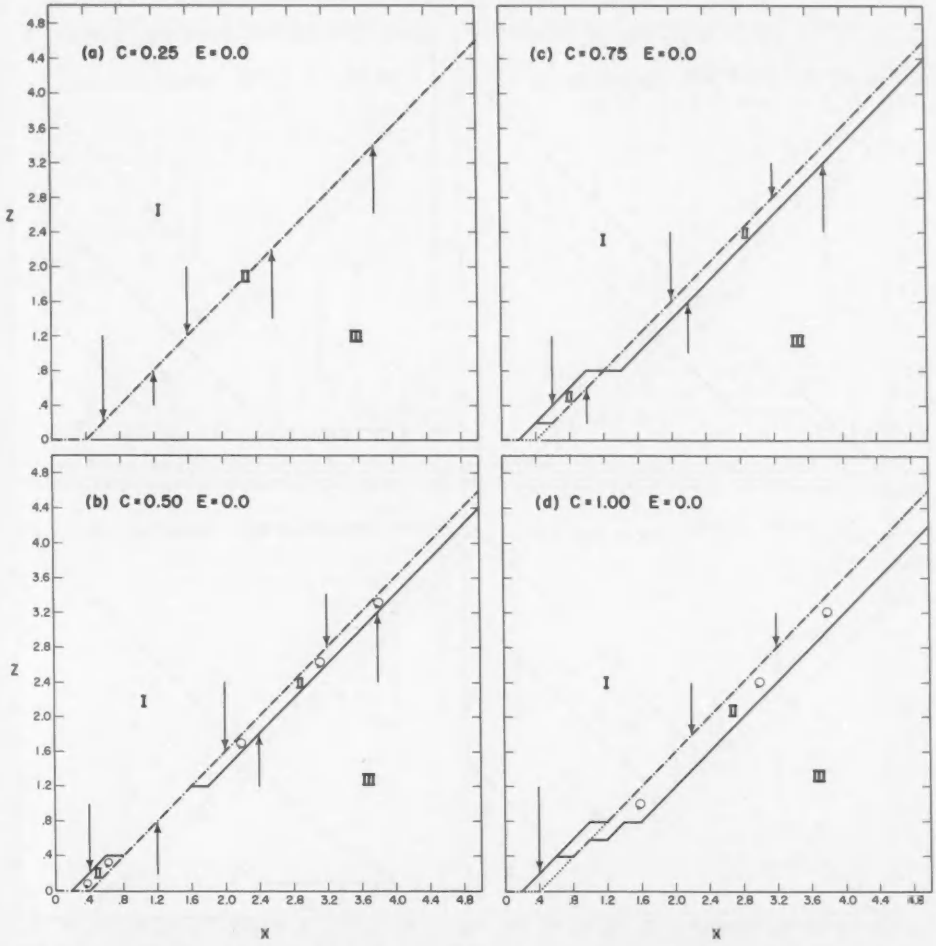

FIGURE 3(a-m).—Optimal policy functions for the Branch River for various assumptions about the relative value of smoothing costs. (See text for details.)

is adaptive, as the prior distribution is updated each period. Moreover, it is not the same as fixing Θ at its estimated value, and using a fixed value of Θ in step 3. The difference can be seen in the integral in Equation (4.1). The reason for considering Bayes equivalent policies is that van Hee (1977a, theorem 3.1) proved that for the models under discussion, when the objective is given by Equation (1.2a) or (1.2b), then the Bayes equivalent policy is optimal for the full Bayes model. For example, in Walters and Hilborn (1976), the parameter Θ is a scalar, i.e., R_2 in our notation. Their problem, for which an optimal policy was not found, can be solved by following a policy outlined in the five steps above.

Many models will not have the necessary structure for a Bayes equivalent policy to be optimal for the full Bayes model, and unlike salmon management, estimates of the population size may not be available every year. A legitimate question is: suppose the present best estimate of Θ were to be used from hereafter. What would be the loss in

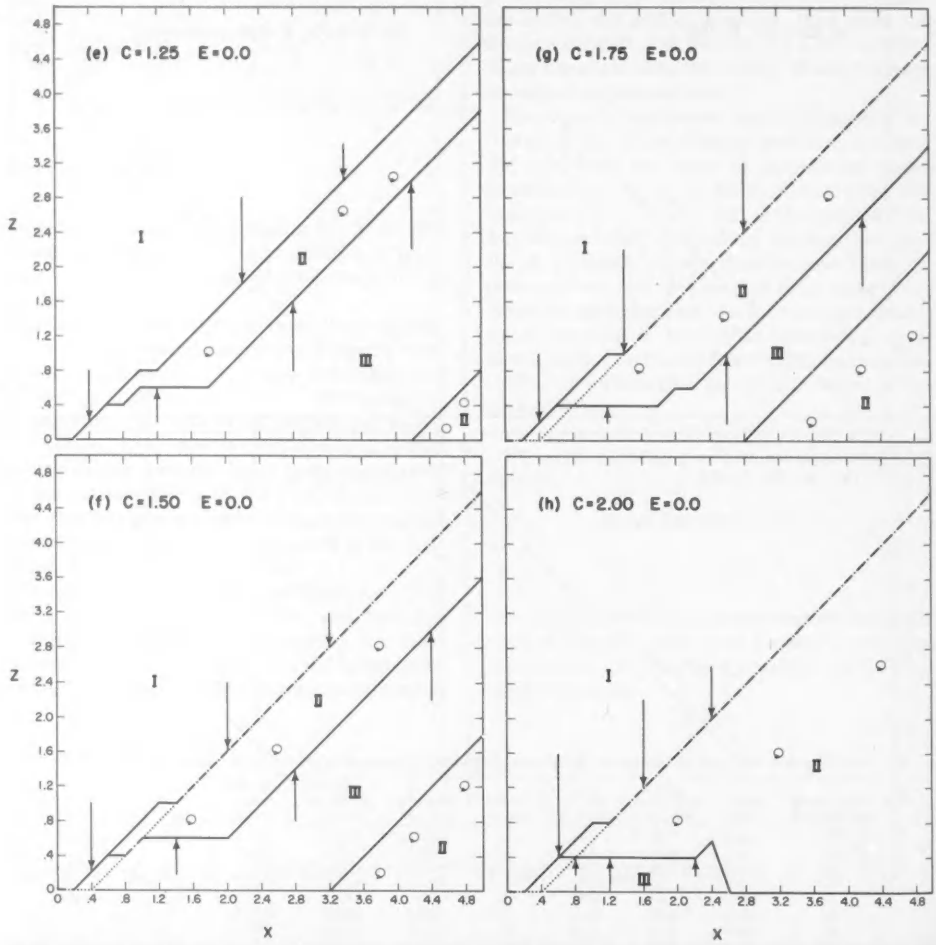

FIGURE 3.—Continued.

expected value? Van Hee (1977b) gave bounds on this expected loss that are easy to compute. To obtain a feel for these bounds, both σ^2 and R_2 are assumed to be random variables. For the Wood River, R_2 could take on the values -0.6, -0.8 and -1.0, and for the Branch River R_2 could take on the values -1.5, -1.85, and -2.00. For the Wood River, σ^2 could assume the values of 0.35, 0.45, and 0.55, and for the Branch River σ^2 could assume the values 0.48, 0.58, and 0.68. Three probability distributions were used as the present prior probability of the parameter values. These were (⅓, ⅓, ⅓,), (¼, ½, ¼), (⅛, ¾, ⅛). The results of the optimization using the parameters at each fixed value (which are needed to calculate the bounds) are given in Table 3. Table 4 gives the bounds on the expected loss of value from using the present estimates of the parameters as in Equation (1.1).

Table 3 suggests that as σ^2 varies for fixed values of R_1, R_2, the mean per period harvest varies little, but the variance of the long-term harvest size distribution increases significantly. As R_2

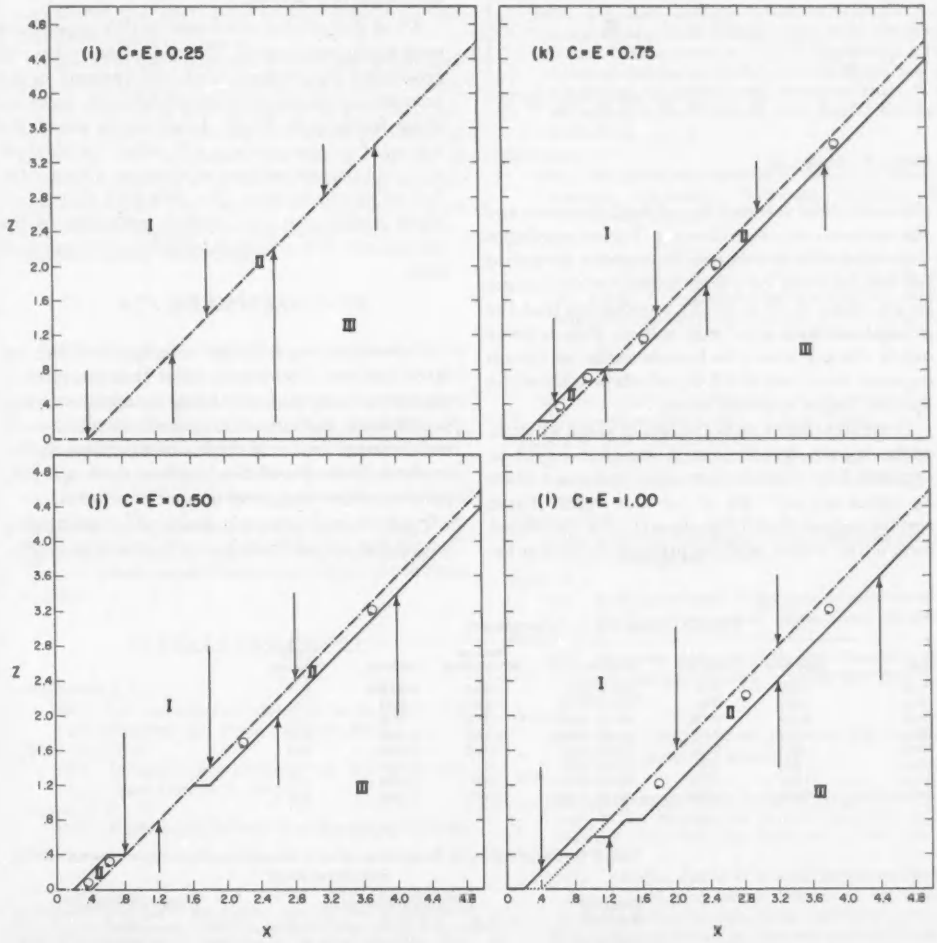

FIGURE 3.—Continued.

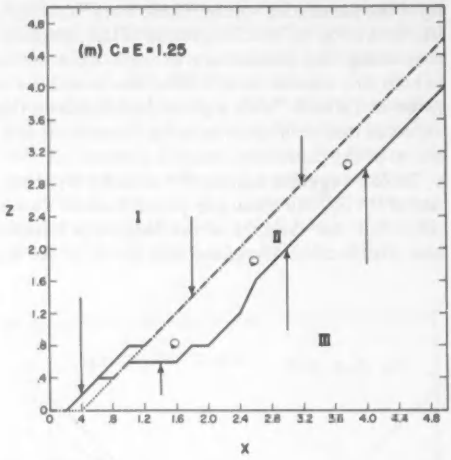

FIGURE 3.—Continued.

varies for fixed values of R_1, σ^2, both the mean and the variance vary significantly. Table 4 reinforces this impression to a degree. If the mean per period harvest does not vary significantly with changes in the value of σ^2, it might be expected that the present estimate of σ^2 will suffice. This is borne out by Table 4, where the bounds on the maximum expected total loss is <0.01, which is <1% of the optimal Bayes expected value.

Some significant expected loss in value when R_2 varies is seen, but the loss is less than might be expected from Table 3. The values in Table 4 when R_2 varies are all <4% of the true value. These results suggest that if Equation (1.1) is the correct form of the model, and the present parameter estimates have relatively small variance, then little is gained in expected value if the more complicated policy is used. The same may not be true if the population size is unobserved.

All of these results suggest a model that is fairly robust to our lack of understanding of nature. A possible explanation for this can be made from the discussion on the effect of grid size. As long as there is some cutoff population size below which no harvesting is allowed, and this cutoff assures that the absorbing state cannot be reached with probability one, then our management can only damage the stocks to a degree.

All of the policies examined in this paper have such a minimum cutoff. The rest of the policy will determine the relative mean and variance of the harvest, and techniques are presented to examine these features in detail. Uncertainty about the values of the parameters will affect the total return, but present estimates often can give a satisfactory approximation. The truly risk adverse decision maker can use present estimates of the parameters that are weighted to be on the cautious side.

SUMMARY

Uncertainty in fisheries management can be faced head on. Techniques exist that allow us to gain much insight on managing randomly varying populations. Optimization procedures allow us to reduce our attention to the few best policies, and to analyze their properties, rather than to pick policies ad hoc that meet no special criteria.

Optimization under uncertainty can also lead to a reconsideration of what is valued in managing a

TABLE 3.—Trials with varied parameters.

River	Value of R_2	Value of σ	Optimal policy	Mean per period harvest	Variance	% time no harvest
Wood	-0.800	0.35	min (x_t, 0.7)	1.0680	0.390976	0.79
Wood	-0.800	0.55	min (x_t, 0.77)	1.2267	1.2422	7.8
Wood	-0.600	0.458	min (x_t, 0.980)	1.5108	1.3136	3.8
Wood	-1.000	0.458	min (x_t, 0.560)	0.9225	0.4839	3.29
Branch	-1.845	0.48	min (x_t, 0.35)	0.6122	0.2253	3.54
Branch	-1.845	0.68	min (x_t, 0.35)	—	—	—
Branch	-1.500	0.579	min (x_t, 0.40)	1.989	0.5254	5.82
Branch	-2.000	0.579	min (x_t, 0.30)	0.9075	0.3068	5.82

TABLE 4.—Largest possible deviation in value of the approximate policy compared with the true Bayes policy.

Probability distribution	When R_2 is uncertain			When σ is uncertain		
	⅓, ⅓, ⅓	¼, ½, ¼	⅛, ¾, ⅛	⅓, ⅓, ⅓	¼, ½, ¼	⅛, ¾, ⅛
Wood River	1.4	0.51	0.5	0.04	0.03	0.03
Branch River	1.04	0.47	0.38	0.01	≤0.01	≤0.01

fishery—in the examples considered, some consistency in the amount harvested is a desirable alternative to high year-to-year fluctuations in the harvest size. But this reduced the average per period catch. Only in extreme situations, where the cost of smoothing out the catch is greater than the unit value of the catch, does any policy resembling MSY become optimal.

Finally, it is possible to obtain an understanding of how robust the management measures are to misspecifications of the underlying model. This is important, since the model is only a guide to our decision making, not the answer. In the models considered, the "best" policies are robust in view of this uncertainty.

A question not examined is the assumption that the population size is observed at the start of each period. This too is usually costly, and inexact. Recently, I and E. J. Sondik developed an efficient algorithm that addresses the relative merits of different sampling intervals for obtaining population estimates.[5] Together, all of these techniques allow for an integrated, realistic approach to management under uncertainty.

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ORGANOCHLORINE RESIDUES IN FISHES FROM THE NORTHWEST ATLANTIC OCEAN AND GULF OF MEXICO

VIRGINIA F. STOUT[1]

ABSTRACT

Residues of ΣDDT (*p,p'*-DDT and its metabolites *p,p'*-TDE and *p,p'*-DDE), PCB (polychlorinated biphenyls), dieldrin, and endrin were determined in the flesh of 700 specimens of fishes caught between 1973 and 1975 in the northwestern Atlantic Ocean and northern Gulf of Mexico off the coasts of the southeastern United States. Species with lowest oil content (<3%)—gag, *Mycteroperca microlepis*; black grouper, *M. bonaci*; red grouper, *Epinephelus morio*; and red snapper, *Lutjanus campechanus*—contained the least amounts of chlorinated hydrocarbon residues. Species with higher oil content—king mackerel, *Scomberomorus cavalla*, (3.5%) and Spanish mackerel, *S. maculatus*, (4.6%)—more consistently contained residues, but still at low levels. Significant correlations ($P<0.05$) were found in red snapper and king mackerel between lipid and size and between lipid and chlorinated hydrocarbon content. The correlations between lipid and PCB in gag and between lipid and DDT in black grouper were also significant. The highest mean values for any species were 0.18 ppm ΣDDT, 0.32 ppm PCB, 0.007 ppm dieldrin, and 0.008 ppm endrin. The highest level in any one composite sample of 10 fish was 1.0 ppm ΣDDT, 1.8 ppm PCB, 0.026 ppm dieldrin, and 0.026 ppm endrin.

Half a century ago manufacturers of surface coatings and of electrical equipment found a common interest in a newly introduced group of organochlorine chemicals, the PCB.[2] These compounds dissolve the inks in carbonless carbon paper, which duplicates without the use of carbon paper. They plasticize the waterproof coatings for dairy silos and fish tanks, and marine antifouling paint. The thermal and electrical properties of PCB are highly desirable in dielectric fluids, the electrical insulators in transformers and capacitors. The PCB are also highly resistant to chemical and biological degradation, and these properties, too, are valued by industrial users.

Immediately following World War II, another organochlorine chemical, DDT, became the magic tool of the medical profession, deeply concerned with preventing outbreaks of infectious, insect-borne diseases. Enormous quantities of DDT were used to prevent epidemics of typhus and plague in war-torn Europe. DDT was dramatically effective in controlling lice and fleas, which carried these diseases. The use of this and related compounds spread rapidly for mosquito and agricultural pest control. Before insect resistance developed, DDT reduced the incidence of malaria to a very low level.

Since PCB and the organochlorine pesticides are not only stable but also easily dispersed in the air and through the water, it is not surprising in retrospect that they are now found even in the polar regions (Sladen et al. 1966; Risebrough et al. 1976; Bowes and Jonkel 1975) and that chlorinated hydrocarbon pollution has become a worldwide problem. Not until the 1960's did appreciation of the adverse effects of these chlorinated hydrocarbons begin to develop. "Silent Spring" (Carson 1962) described the effects on the environment of the accumulation of DDT, and Jensen (Anonymous 1966; Jensen et al. 1969) found PCB in marine animals. Burdick et al. (1964) noted reproductive failure in lake trout when the eggs contained a high level of ΣDDT. Aulerich et al. (1973) traced the reproductive failure and mortality in ranch-grown mink back to coho salmon, *Oncorhynchus kisutch*, from Lake Michigan and ultimately to the PCB they contained. Only recently fin erosion, a disease associated with municipal and industrial discharges, was related to ΣDDT (Mearns and Sherwood 1977). Montrose Chemical Company released wastes from DDT manufacture directly into

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[2]Abbreviations used in this manuscript: DDE = *p,p'*-dichlorodiphenyldichloroethylene; DDMU = *p,p'*-dichlorodiphenylchloroethylene; DDT = *p,p'*-dichlorodiphenyltrichloroethane; PCB = polychlorinated biphenyls; Σ DDT = DDT and its metabolites DDE and TDE; TDE = *p,p'*-dichlorodiphenyldichloroethane.

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the Los Angeles County sewer system which flows via sewer outfalls into the marine environment of southern California. From this unanticipated source of ΣDDT pollution, high levels of ΣDDT developed throughout the southern California marine environment from mollusks (Young et al. 1976), crustaceans (Burnett 1971), and fishes (McDermott-Ehrlich et al. 1978) to marine birds (Anderson et al. 1975) and cetaceans (Le Boeuf and Bonnell 1971). Henderson et al. (1969, 1971) found organochlorine residues in freshwater fishes throughout the United States. Some species of freshwater fishes, especially those from the Great Lakes, contained levels of chlorinated hydrocarbons that exceeded the U.S. Food and Drug Administration guidelines (Reinert 1970; Veith 1975). In recent years, the use of chlorinated hydrocarbons has been drastically curtailed, but concern remains about the continuing occurrence of these toxic compounds in the marine environment.

Fishes and shellfishes are excellent organisms for monitoring chlorinated hydrocarbons. Shellfishes have been used as indicators of short-term pollution (Butler 1973; Goldberg et al. 1978) because they accumulate and depurate these substances readily. Fishes, on the other hand, reflect long-term exposure since they lose chlorinated hydrocarbons slowly, if at all (Lieb et al. 1974). Butler and Schutzmann (1978) have reported on pesticides and PCB in yearling estuarine fishes of the United States. Outside of their study, however, few data on fishes for human consumption from the western Atlantic Ocean have been published except on fishes from Canadian waters (Sims et al. 1977). The study reported here was undertaken to obtain information about levels of ΣDDT, PCB, dieldrin, and endrin in fillets from fishes caught in the northwestern Atlantic Ocean and northern Gulf of Mexico. Six marine species of both commercial and sport value have been examined.

METHODS

Samples of gag, *Mycteroperca microlepis*; black grouper, *M. bonaci*; red grouper, *Epinephelus morio*; red snapper, *Lutjanus campechanus*; king mackerel, *Scomberomorus cavalla*; and Spanish mackerel, *S. maculatus*, were collected from the northwestern Atlantic Ocean and northern Gulf of Mexico, from Beaufort, N.C., south to the Florida Keys, and west to Aransas Pass, Tex. Sampling occurred between October 1973 and October 1975, but mainly in 1975. Specimens were frozen and held at −18° C. They were thawed for filleting, grinding, compositing, and refrozen until analysis. In the aggregate, 70 samples each containing 10 fish of the same species and of similar size were obtained. Each sample was a composite of equal weights of ground skinless fillets from the 10 individual fish. At most sites, two or three samples from different size fish were selected. The collection sites, size, and lipid content of the specimens are listed in Table 1.

Extracts were prepared by the procedures of Reinert (1970). Samples for ΣDDT and PCB analysis were extracted with propanol-2/benzene (1:1), and the extracted materials transferred to hexane by repeated codistillation of the propanol-2, benzene, and water with hexane. One aliquot of the hexane extract was evaporated to minimum weight for determination of the lipid content. Another aliquot was cleaned up on Florisil.[3] PCB were separated from TDE, DDT, and most of the DDE on activated silica gel (Snyder and Reinert 1971), which also separates the interfering hydrocarbons, phenanthrene, fluoranthrene, and pyrene from the PCB (Zitko 1978). At least 90% of the PCB was contained in the pentane fraction, which also contained part of

[3]Mention of specific products or companies in this paper does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Collection sites, size, and lipid content of fishes from the northwest Atlantic Ocean and Gulf of Mexico.

Species	Sites[1]	No.[2]	Fork length (cm) Mean	Fork length (cm) Range[3]	Weight (kg) Mean	Weight (kg) Range[3]	Lipid content (%) Mean	Lipid content (%) Range[3]
Gag	1, 2, 3	8	86	64-108	9.77	3.79-18.32	2.9	0.2-5.9
Black grouper	5, 6	6	77	54- 96	7.01	1.98-12.70	0.6	0.2-1.2
Red grouper	1, 4, 5, 6	10	68	52- 82	6.08	2.42-11.50	0.5	0.1-1.0
Red snapper	1, 2, 3, 4, 5, 6, 7, 8	18	65	45- 83	5.94	1.65-11.35	1.5	0.4-3.9
King mackerel	1, 2, 3, 4, 5, 6, 9	18	87	55-119	6.01	1.20-12.91	3.5	0.4-7.5
Spanish mackerel	3, 4, 5, 6, 7	10	54	45- 64	1.41	0.48- 2.34	4.6	1.7-9.4

[1]1 - Beaufort, N.C.; 2 - Savannah, Ga.; 3 - Florida, East Coast; 4 - Florida Keys; 5 - Tampa/St. Petersburg, Fla.; 6 - Panama City, Fla.; 7 - Mobile, Ala.; 8 - Pascagoula, Miss.; 9 - Aransas Pass, Tex.
[2]Number of composites, each consisting of 10 fish.
[3]Range of means of individual composites.

the DDE. All of the TDE and DDT eluted into the benzene fraction. For dieldrin and endrin analysis, tissues were saponified with KOH in aqueous ethanol, extracted with hexane, and cleaned up on Florisil. Since the specimens, originally collected for trace-metal analysis, were stored in polypropylene containers (Falcon No. 4014) with polyethylene lids (Falcon No. 4017), the containers and lids were also analyzed to assure freedom from interfering substances. The details of our procedures were published previously (Stout and Beezhold 1979). Blanks carried through the whole procedure for either PCB and ΣDDT or dieldrin and endrin showed no chromatographic peaks which interfered with quantitation of the chlorinated hydrocarbons.

The extracts of the fishes were quantitated by electron-capture gas chromatography. A Varian 600 C gas chromatograph with a titanium tritide detector was fitted with a 1.5 m (5 ft) × 0.32 cm (0.125 in) o.d. glass column containing a mixture of equal parts of 15% QF-1 on 80-100 mesh Gas Chrom Q and 10% DC-200 on the same support (Burke and Holswade 1966). Reference standards of *p,p'*-DDE, *p,p'*-DDMU, *p,p'*-TDE, *p,p'*-DDT, dieldrin, and endrin were obtained from the U.S. Environmental Protection Agency, Health Effects Research Laboratory, Research Triangle Park, N.C. Aroclor 1254 obtained from the Monsanto Company, St. Louis, Mo., was the standard for the PCB because the residues in the fishes matched this Aroclor most closely. Standard curves of peak height versus concentration were used to determine the concentrations of components in the extracts. The sensitivity throughout each run was assured by frequent injections of standard solutions. The quantifiable limit was about 0.003 ppm for DDE, TDE, DDT, dieldrin, and endrin, and about 0.04 ppm for PCB depending on daily sensitivity. The mean relative standard deviation for samples analyzed in duplicate was 11%. The average recovery of samples spiked with standards was 85%. The values reported were not corrected for recovery. Residue values were calculated on the basis of micrograms chlorinated hydrocarbon per gram wet tissue or parts per million (ppm).

The PCB were quantitated by summing the peak heights corresponding to the five major peaks in Aroclor 1254 after omitting the twin peak with a retention time similar to that of *p,p'*-DDE. As Veith (1975) also concluded, use of five peaks increased the accuracy of PCB measurement by reducing the effect of minor variations in concentration of individual components in the samples (Figure 1).

Since part of the DDE eluted from silica gel with the PCB fraction and one of the major peaks in Aroclor 1254 overlapped the DDE peak in the gas-chromatographic traces, a special technique was needed to quantitate the DDE in the PCB fraction. First the gross DDE concentration was determined in the usual way from the peak height versus DDE concentration curve. Next, the contribution of PCB to that overlapping peak was calculated based on the assumption that the height of Aroclor peak 3, the peak which overlapped DDE, was proportional to the heights of the five PCB peaks used to calculate the concentration of PCB. To make this calculation, the sum of the peak heights of the five major PCB peaks excluding the "DDE" peak was plotted against the peak height of the "DDE" peak in PCB standards of increasing concentrations. From the sum of the five PCB peaks in the sample, the peak height of the PCB portion of peak 3 in that sample was determined. This peak height was converted to concentration of DDE via the peak height versus concentration curve for DDE. The apparent concentration of DDE from PCB peak 3 was subtracted from the gross DDE concentration in the "DDE" peak to obtain the net concentration of DDE in the PCB fraction. The elctron-capture detector is so much more sensitive to DDE than PCB that this method of calculation affected the accuracy of DDE determination only to a small extent (Figure 1). Use of a minicomputer expedited these calculations.

Confirmation of DDT and its metabolites and PCB was effected by saponifying separate portions of tissue (Reinert 1970). DDT is dehydrochlorinated by base to DDE, and TDE similarly to DDMU. PCB are stable to base. The levels of dieldrin and endrin were too low to warrant confirmation studies.

RESULTS AND DISCUSSION

The marine fishes from the northwestern Atlantic Ocean and northern Gulf of Mexico analyzed in this study contained relatively low levels of ΣDDT and PCB. Of the 70 composite samples, only 29 contained more than 0.05 ppm ΣDDT and 0.1 ppm PCB in the edible portion (skinless fillets), and only one as much as 1 ppm ΣDDT and PCB. Red grouper contained the lowest levels of both chlorinated hydrocarbons. The mean ΣDDT content for

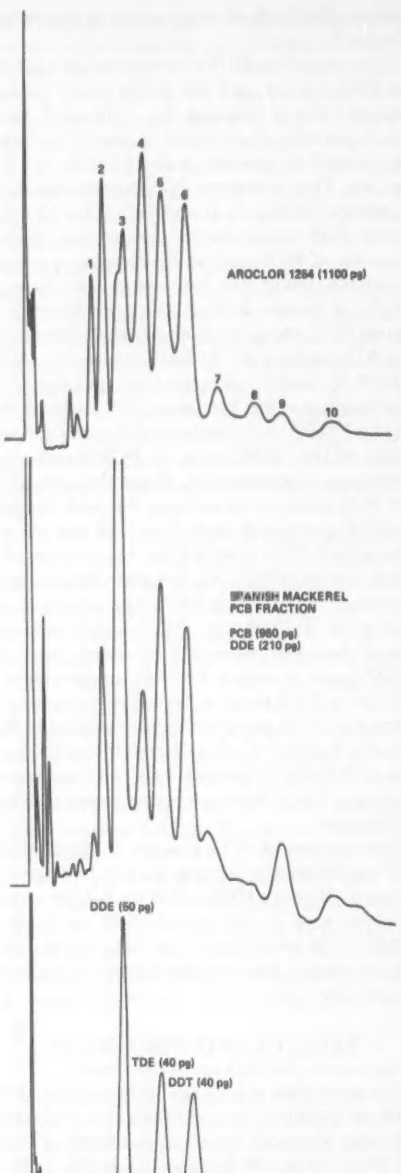

FIGURE 1.—Gas chromatographic curves of Aroclor 1254, the PCB fraction of an extract from Spanish mackerel, and DDT and its metabolites DDE and TDE; pg = picograms or 10^{-12} g.

10 sets of red grouper was 0.008 ppm; for most samples, PCB were not detectable. Black grouper and gag contained slightly higher levels of ΣDDT and PCB. Red snapper also contained little ΣDDT (mean 0.039 ppm), but the PCB level in six samples exceeded 0.1 ppm. Only the two species of mackerel consistently contained quantifiable amounts of both ΣDDT and PCB. The mean levels of ΣDDT were 0.144 ppm in Spanish mackerel and 0.177 ppm in king mackerel. The mean PCB level in both species of mackerel was 0.32 ppm. The highest levels of both chlorinated hydrocarbons were found in one composite sample of king mackerel from the Florida Keys, 0.996 ppm ΣDDT and 1.8 ppm PCB. The data are summarized in Table 2.

The limited data in the literature convey a similar picture. Groupers of the genera *Epinephelus* and *Mycteroperca* from the Gulf of Mexico and the Grand Bahamas contained 0-0.10 ppm ΣDDT and 0.003-0.22 ppm PCB in muscle (Giam et al. 1974). Red snapper from Mobile Bay, Ala., contained 0.086 ppm ΣDDT and 0.14 ppm PCB in the whole animal; gray snapper, *Lutjanus griseus*, from Jacksonville, Fla., 0.007 ppm ΣDDT and no PCB in the whole animal (Markin et al. 1974). Small Spanish mackerel (306 g) from the Savannah River estuary in Georgia contained neither ΣDDT nor PCB in muscle. (Butler[4]) Although somewhat larger than those fish, the smallest fish in the current study (475 g) contained barely detectable amounts of these substances (0.008 ppm ΣDDT and 0.034 ppm PCB). Markin et al. (1974) found 0.04-0.16 ppm ΣDDT and <0.01-0.18 ppm PCB in seven whole Spanish mackerel from the southeastern United States. A single sample of king mackerel muscle from the Gulf of Mexico off Mexico contained 0.024 ppm ΣDDT and 0.034 ppm PCB (Giam et al. 1972). Atlantic mackerel, *Scomber scombrus*, collected in 1971-72 in Canadian waters (Sims et al. 1977) contained more ΣDDT (0.26 ppm) and PCB (0.41 ppm) in the "edible portion" (which may have contained skin and/or bones) than did skinless fillets of either species of mackerel examined in my study. On the other hand, muscle from Atlantic mackerel from the Bay of Fundy-Gulf of Maine contained the same level of PCB (0.35 ppm) (Zitko et al. 1972).

The proportions of *p,p'*-DDT and its metabolites were very similar in the king and Spanish mackerel examined in our study. *p,p'*-DDE is the

[4]Butler, P. A. 1978. EPA-NOAA Cooperative Estuarine Monitoring Program, Final Report, Gulf Breeze, Fla., 108 p.

TABLE 2.—ΣDDT and PCB in fishes from the northwest Atlantic Ocean and Gulf of Mexico. nq = not quantifiable; nd = none detected.

Species	No.[1]	ΣDDT (ppm) Mean±SD	ΣDDT (ppm) Range	PCB (ppm) Mean±SD	PCB (ppm) Range
Gag	8	0.036±0.013	0.017-0.050	0.087±0.023	nq-0.129
Black grouper	6	0.009±0.007	0.003-0.020	nq	nq-0.059
Red grouper	10	0.008±0.007	n.d.-0.025	nd	nd-nq
Red snapper	18	0.039±0.076	n.d.-0.322	0.121±0.108	nd-0.464
King mackerel	18	0.177±0.239	0.009-0.996	0.322±0.414	0.060-1.78
Spanish mackerel	10	0.144±0.097	0.008-0.319	0.319±0.263	0.034-0.821

[1]Number of composites, each consisting of 10 fish.

major component (~65%) accompanied by about 25%of the parent compound and 10% *p,p'*-TDE. Although the composite picture for red snapper looked markedly different (Table 3), in fact the DDT residues in that species actually fell into two categories. In the first group, *p,p'*-TDE and *p,p'*-DDT were not quantifiable, and the maximum content of *p,p'*-DDE was 0.029 ppm. In the second group, five samples containing >0.029 ppm *p,p'*-DDE, both *p,p'*-TDE and *p,p'*-DDT were quantifiable. In those five samples, the proportions of the three components were the same as in the mackerel. Finfish from the Atlantic coast of Canada (Sims et al. 1977) contained proportionately much less *p,p'*-DDE (45%) and more *p,p'*-DDT (40%) and *p,p'*-TDE (15%). The increase in the proportion of *p,p'*-DDE in the present samples may reflect degradation of the parent compound in the environment before it accumulated in the fishes. Samples for the Canadian study were collected in 1971 and 1972, soon after usage of DDT had been drastically curtailed (around 1970) as the result of increasing insect resistance, problems with indirect contamination of foodstuffs, and concern about effects of DDT on nontarget species. Several years elapsed before the samples for the present study were collected, mainly in 1975. In the interval, DDT was degrading aerobically to DDE and anaerobically in the marine environment to TDE. Alternatively, DDT may metabolize more rapidly to DDE in the more temperate climate of the region studied and somewhat less rapidly to TDE.

TABLE 3.—Mean proportions of ΣDDT present as *p,p'*-DDE, *p,p'*-TDE, and *p,p'*-DDT in fishes from the northwest Atlantic Ocean and Gulf of Mexico.

Species	*p,p'*-DDE (%) Mean±SD	*p,p'*-DDE (%) Range	*p,p'*-TDE (%) Mean±SD	*p,p'*-TDE (%) Range	*p,p'*-DDT (%) Mean±SD	*p,p'*-DDT (%) Range
Red snapper, all	88±18	58-100	3±5	0-15	9±13	0-30
Red snapper[1]	62± 6	58- 72	10±3	7-15	28± 4	21-32
King mackerel	64± 8	48- 77	8±6	0-17	28± 6	16-40
Spanish mackerel	66±19	48-100	12±8	0-24	21±12	0-37

[1]Five samples which contained >0.029 ppm DDE.

The concentration of PCB, when present, was higher than that of ΣDDT in all samples but one. The mean ratio of PCB to ΣDDT was 1.8 for gag, 2.2 for king and Spanish mackerel, and 2.6 for six sets of red snapper. In the two other samples of red snapper with quantifiable levels of PCB, the PCB/ΣDDT ratios were 22.7 and 24.3. The concentrations of ΣDDT were below 0.01 ppm in both cases. The one sample of red snapper in which the PCB/ΣDDT ratio was below 1 contained a relatively large amount of ΣDDT, 0.096 ppm, the second highest ΣDDT value in the 18 samples of red snapper. In contrast, the PCB concentration was low both in absolute amount, <0.06 ppm, and in rank, 14th out of 18 samples.

The chlorinated-hydrocarbon content of the specimens in this study was, in general terms, directly related to the lipid content. The groupers, which contained <1% lipid, contained the least ΣDDT and PCB. King and Spanish mackerel had the highest lipid contents, 3.5 and 4.6%, respectively, and the highest levels of both ΣDDT and PCB. In three of the six species, the correlation between lipid and ΣDDT was significant, i.e., $P<0.05$. Similarly, in three of the four species for which PCB were quantifiable the correlation between lipid and PCB was significant. Possible relationships between size and chlorinated hydrocarbon content were also examined. Although length, weight, ΣDDT, and PCB were all studied, in no case was a significant correlation found in any of the six species (Table 4). In two of the six species, the correlations between length and lipid and also between weight and lipid were significant. In both species, red snapper and king mackerel, the *P* values for lipid versus chlorinated hydrocarbon, were below 0.01. Giam et al. (1974) noted a relationship between size and concentration of pollutants in groupers from the Gulf of Mexico, but only in the area with the highest contamination, i.e., up to 0.1 ppm.

ΣDDT and PCB levels within single species were compared at the various sites. Fish from the

TABLE 4.—Sample correlation and coefficients (R) and their significance (P) between body dimensions, lipids, and organochlorine residues in fishes from the northwest Atlantic Ocean and Gulf of Mexico.

Species	No.[1]	Length vs. lipid		Weight vs. lipid		Length vs. ΣDDT		Weight vs. ΣDDT		Lipid vs. ΣDDT		Length vs. PCB		Weight vs. PCB		Lipid vs. PCB	
		R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P
Gag	8	−0.369	0.368	−0.317	0.444	[2]0.189	0.653	[2]0.232	0.580	[2]0.552	0.156	0.085	0.842	0.117	0.782	0.755	0.030
Black grouper	6	0.102	0.847	0.056	0.917	[2]0.426	0.400	[2]0.356	0.489	[2]0.896	0.016		[3]		[3]		[3]
Red grouper	10	0.536	0.110	0.595	0.070	[2]0.576	0.082	[2]0.511	0.132	[2]−0.256	0.476		[3]		[3]		[3]
Red snapper	18	0.571	0.013	0.663	0.003	[2]0.323	0.191	[2]0.438	0.069	[2]0.688	0.002	0.296	0.233	0.374	0.126	0.716	0.001
King mackerel	18	0.575	0.013	0.598	0.009	0.357	0.146	0.333	0.176	0.722	0.001	0.344	0.162	0.333	0.177	0.694	0.001
Spanish mackerel	10	−0.035	0.923	−0.117	0.747	0.468	0.173	0.417	0.231	0.159	0.661	0.214	0.552	0.209	0.562	0.306	0.390

[1]Number of composites, each consisting of 10 fish.
[2]DDE only, because TDE and DDT not always quantifiable.
[3]PCB not quantifiable.

Florida Keys contained the greatest amounts of both substances, indicating that contamination from agricultural and domestic effluents was greatest in south Florida, an area of intense agriculture and relatively dense population as well. Fish caught in the vicinity of Beaufort and Mobile contained slightly less ΣDDT and PCB. Fish from the other sites contained lower levels of chlorinated hydrocarbons, which were not distinguishable by site, except that only DDE was quantifiable in the one sample from Pascagoula, Miss. The Mississippi River, which receives the runoff from 40% of the land mass of the conterminous United States, including the corn belt and the cotton belt, did not seem to be the main source of either ΣDDT or PCB.

Low levels of dieldrin and endrin, two highly toxic organochlorine pesticides, were found in the fish included in this study. The highest concentration of either compound was 0.026 ppm. The dieldrin and endrin content of only the three species with the highest levels of ΣDDT and PCB were determined. Nonetheless, dieldrin and endrin were quantifiable only in about one-third of the samples. Two of 18 red snapper, 7 of 18 king mackerel, and 6 of 10 Spanish mackerel samples contained quantifiable amounts of both compounds. The mean levels for Spanish mackerel, the species with the highest mean concentrations, were 0.007 ppm dieldrin and 0.008 ppm endrin (Table 5). King mackerel from Aransas Pass contained the highest concentration of dieldrin, 0.026 ppm; Spanish mackerel from Panama City, Fla., the highest concentration of endrin, also 0.026 ppm. The dieldrin and endrin concentrations in the three species followed the same distribution patterns with relation to species and lipid content as was observed for ΣDDT and PCB. Butler (see footnote 4) found no dieldrin in the muscle of small Spanish mackerel from the Savannah River estuary.

CONCLUSIONS

Residues of ΣDDT, PCB, dieldrin, and endrin, although generally low, were found in all species and all locations except Pascagoula, Miss., where only DDE was quantifiable. The highest levels of ΣDDT and PCB, and the only ones to reach 1 ppm, were in one composite sample of king mackerel from the Florida Keys, 0.996 ppm ΣDDT and 1.8 ppm PCB. The highest level of dieldrin, 0.026 ppm, was in king mackerel from Aransas Pass, Tex., and of endrin, also 0.026 ppm, in Spanish mack-

TABLE 5.—Dieldrin and endrin in fishes from the northwest Atlantic Ocean and Gulf of Mexico. nd = not detected; nq = not quantifiable.

Species	No.[1]	Dieldrin (ppm) Mean±SD	Dieldrin (ppm) Range	Endrin (ppm) Mean±SD	Endrin (ppm) Range
Red snapper	18	nd	nd-nq	nd	nd-0.003
King mackerel	18	0.005±0.006	nd-0.026	0.004±0.004	nd-0.014
Spanish mackerel	10	0.007±0.004	nd-0.014	0.008±0.010	nd-0.026

[1]Number of composites, each consisting of 10 fish.

erel from Panama City, Fla. The species with the highest lipid contents contained the highest concentrations of chlorinated hydrocarbons. Significant correlations ($P<0.05$) were found between lipid and size and between lipid and chlorinated hydrocarbon content in two of the six species. In two other species the correlation between lipid and either ΣDDT or PCB was significant. In all cases but one, the chlorinated hydrocarbon levels were substantially below the U.S. Food and Drug Administration guidelines: 5 ppm ΣDDT, 2 ppm PCB, and 0.3 ppm dieldrin and endrin.

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SYSTEMATICS AND DISTRIBUTION OF CERATIOID ANGLERFISHES OF THE FAMILY MELANOCETIDAE WITH THE DESCRIPTION OF A NEW SPECIES FROM THE EASTERN NORTH PACIFIC OCEAN[1]

THEODORE W. PIETSCH AND JOHN P. VAN DUZER[2]

ABSTRACT

The ceratioid anglerfish family Melanocetidae is revised on the basis of a study of approximately 600 specimens collected from all oceans. Of the 11 nominal species of *Melanocetus* based on females, 4 are recognized: *M. johnsoni*, with *M. krechi*, *M. rotundatus*, *M. ferox*, *M. cirrifer*, and *M. megalodontis* as synonyms; *M. polyactis*; *M. niger*; and *M. murrayi*, with *M. vorax* and *M. tumidus* as synonyms. A fifth species is newly described from a single female collected from the eastern Pacific Ocean off Mazatlán, Sinaloa, Mexico. The new form differs most strikingly from its allies in having a larger escal bulb and shorter jaw teeth.

Melanocetus is widely distributed throughout all the major oceans of the world between about 250 m and some unknown lower depth limit that exceeds 3,000 m. *Melanocetus johnsoni* and *M. murrayi* are wide ranging forms, whereas *M. polyactis* and *M. niger* are apparently restricted to the eastern tropical Pacific.

Melanocetus murrayi appears to be the most phylogenetically derived member of the family. The four remaining species are much more closely related to each other than any is to *M. murrayi*. *Melanocetus johnsoni* is perhaps derived in having a relatively long illicium, and in having fewer, but longer jaw teeth. *Melanocetus polyactis* and *M. niger* are similar in having relatively short jaw teeth, a similar escal morphology, and a sympatric geographic distribution that is limited to the eastern tropical Pacific. The newly described form is derived in having an extremely large escal bulb, comparable with no other known ceratioid.

The Melanocetidae include globose, bathypelagic anglerfishes, easily separated from members of allied families by having 12 or more dorsal fin rays, 3 or 4 anal rays, and large, fanglike jaw teeth (Bertelsen 1951; Pietsch 1972a). The only recognized genus of the family was established by Günther (1864) with the description of *Melanocetus johnsoni*, based on a single female specimen collected in the Atlantic Ocean, off Madeira. Since that time, 10 additional species based on females have been described (Table 1). From a comparison of the characters used to distinguish these nominal forms, Bertelsen (1951, table 4) doubted that *M. krechi* and *M. cirrifer* could be maintained and that *M. ferox* and *M. niger* might be synonyms. *Melanocetus murrayi* and *M. johnsoni* were recognized as the only species known from the Atlantic; *M. niger*, *M. ferox*, and *M. polyactis* were considered forms restricted to the eastern tropical Pacific. Six larval specimens from the Gulf of Panama were assigned to *M. polyactis*. The remaining larvae (approximately 600 individuals) were separated into two groups, representing *M. murrayi* and *M. johnsoni*, on the basis of geographic distribution, fin ray counts, and a comparison of larval and adolescent female pigmentation. Despite these allocations, Bertelsen (1951) made it clear that ". . . the separation of the species is still very uncertain and future investigations and material will probably make it necessary to revise this synopsis."

At the time of Bertelsen's (1951) monograph on the Ceratioidei, 19 metamorphosed melanocetid males were known. Of these, 14 had been set up as types of 12 separate species, and 5 were uncertainly placed. On the basis of subdermal pigment, fin ray counts, and geographic distribution, Bertelsen (1951) synonymized 6 of these 12 nominal forms with *M. johnsoni* and 4 with *M. murrayi*. The remaining two species based on males, *M. longirostris* and *M. nudus*, each differing slightly from the rest of the material, were tentatively retained (Table 1).

With the vast increase in the amount of material of *Melanocetus* made available in the last 25

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TABLE 1.—Reallocation of nominal forms of *Melanocetus*. Valid names on right. Synonymy for species based on males after Bertelsen 1951.

Females:	
Melanocetus johnsoni Günther 1864	*Melanocetus johnsoni* Günther 1864
Melanocetus krøchi Brauer 1902	
Melanocetus rotundatus Gilchrist 1903	
Melanocetus farox Regan 1926	
Melanocetus cirrifer Regan and Trewavas 1932	
Melanocetus megalodontis Beebe and Crane 1947	
Melanocetus polyactis Regan 1925	*Melanocetus polyactis* Regan 1925
Melanocetus niger Regan 1925 (in part)	*Melanocetus niger* 1925
Melanocetus niger Regan 1925 (in part)	
Melanocetus murrayi Günther 1887	*Melanocetus murrayi* Günther 1887
Melanocetus vorax Brauer 1902	
Melanocetus tumidus Parr 1927	
Males:	
Centrocetus spinulosus Regan and Trewavas 1932	*Melanocetus johnsoni* Günther 1864
Xenoceratias micracanthus Regan and Trewavas 1932	
Xenoceratias heterorhynchus Regan and Trewavas 1932	
Xenoceratias laevis Regan and Trewavas 1932	
Xenoceratias brevirostris Regan and Trewavas 1932	
Xenoceratias braueri Koefoed 1944	
Rhynchoceratias rostratus Regan 1926 (in part)	*Melanocetus polyactis* Regan 1925
Rhynchoceratias leucorhinus Regan 1926 (in part)	
Rhynchoceratias acanthirostris Parr 1927	*Melanocetus murrayi* Günther 1887
Rhynchoceratias latirhinus Parr 1927	
Rhynchoceratias longipinnis Parr 1930	
Xenoceratias regani Koefoed 1944	

yr, we are able to recognize five species based on females. Four of these are previously described forms: *M. johnsoni*, represented by 346 specimens collected from all three major oceans of the world; *M. polyactis* and *M. niger*, known from 15 and 6 specimens both restricted to the eastern tropical Pacific; and *M. murrayi*, 140 specimens of worldwide distribution. The fifth is a new species recently collected by the *Velero IV* of the University of Southern California in the eastern Pacific off Mazatlán, Sinaloa, Mexico. It differs strikingly from its allies in having a considerably larger escal bulb and shorter jaw teeth.

Although the number of known male specimens has increased nearly fourfold since Bertelsen's (1951) work, no new diagnostic data are available. We have examined 73 individuals (11.5-24 mm standard length), none of which can be satisfactorily identified to species based on females. As predicted by Bertelsen (1951), the variation in the number of denticular teeth is greater than previously thought and values given in his key overlap to a much greater extent than is indicated. An attempt to utilize differences in larval pigmentation, thought to be more or less retained, at least in the younger metamorphosed males, failed to separate the material into groups that could be associated with species based on females. Although Bertelsen's (1951) synonymies for nominal species based on males are retained here, additional male specimens are listed as *Melanocetus* sp.

METHODS AND MATERIALS

Standard lengths (SL) are used throughout unless otherwise stated. Measurements were taken from the left side whenever possible and rounded to the nearest 0.5 mm. To ensure accurate fin ray counts, skin was removed from the pectoral fins and incisions were made to reveal the rays of the dorsal and anal fins. Sockets, indicating missing teeth in the jaws and on the vomer, were included in total tooth counts. Jaw tooth counts are the sum of both right and left sides. Head depth is the distance from the tip of the sphenotic spine to the base of the quadrate spine. Head width is the distance between the anterolateralmost margins of the sphenotic bones. Lower jaw length is the distance from the symphysial spine to the posteriormost margin of the articular. Illicium length is the distance from the articulation of the pterygiophore of the illicium and the illicial bone to the distal surface of the esca, excluding escal appendages. The width of the pectoral fin lobe is the distance between the point of articulation of the uppermost fin ray to the articulation of the lowermost fin ray. Terminology used in describing the various parts of the angling apparatus follows Bradbury (1967). Definitions of terms used for the different stages of development follow Bertelsen (1951). Complete locality data are given for primary type material only.

The comparative osteological investigation was

based primarily on five female specimens (two *M. murrayi*, 75 and 84 mm SL, and three *M. johnsoni*, 44.5, 60, and 75 mm SL; material representing the remaining species of the genus was unavailable) cleared and stained with Alizarin red S following the trypsin digestion technique (Taylor 1967). Bone terminology follows Pietsch (1974).

Unless otherwise indicated, all diagnoses and descriptions are based on female specimens >20 mm SL. For males and larvae see Bertelsen (1951). Material is catalogued in the following institutions: Australian Museum, Sydney (AMS); British Museum (Natural History), London (BMNH); Bingham Oceanographic Collections, Peabody Museum of Natural History, Yale University (BOC); California Academy of Sciences, San Francisco (CAS); Florida State Museum, University of Florida, Gainsville (FSM); Institute of Oceanology, Academy of Sciences, U.S.S.R., Moscow (IOAN); Institute of Oceanographic Sciences, Surrey, England (IOS); Institut für Seefischerei, Hamburg (ISH); Natural History Museum of Los Angeles County (LACM); Museum of Comparative Zoology, Harvard University (MCZ); National Museum of New Zealand, Wellington (NMNZ); Royal Ontario Museum, Toronto (ROM); South African Museum, Cape Town (SAM); University of Bergen, Zoological Museum (UBZM); University of Miami Marine laboratory, (UMML); National Museum of Natural History, Washington, D.C. (USNM); Virginia Institute of Marine Science, Gloucester Point (VIMS); Zoological Museum, Humboldt University, Berlin (ZMHU); Zoological Museum, University of Copenhagen (ZMUC).

OSTEOLOGY OF FEMALES

The osteology of *Melanocetus* was partially described by Regan (1926, fig. 10), Parr (1930a, fig. 2-5, male only), Regan and Trewavas (1932, fig. 19-28), and Bertelsen (1951, fig. 13, 14). In the following account, only those comparative aspects that need amending or that have not previously appeared in the literature are discussed.

Cranium (Figures 1-9). — The anterior portion of the cranium of *Melanocetus* is considerably wider, relative to the posterior portion, than in other ceratioids; the distance between the lateral margins of the ethmoid cartilage is nearly equal to the

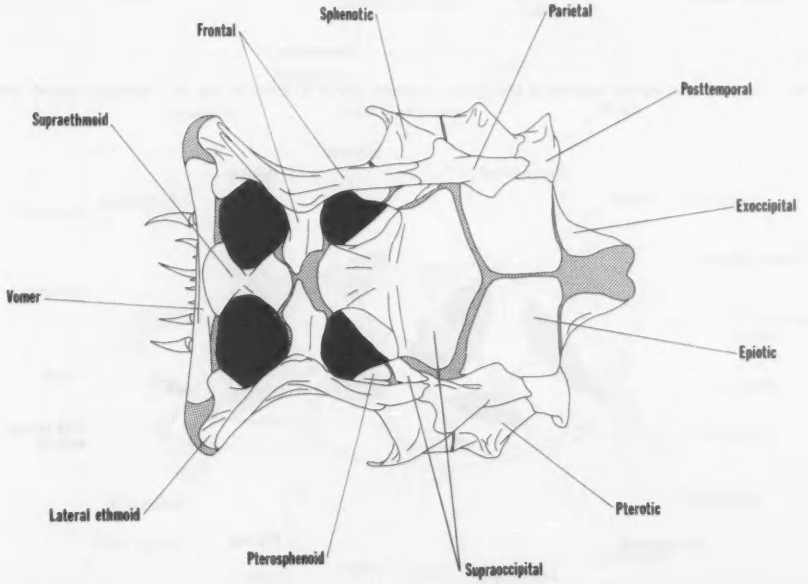

FIGURE 1.—Dorsal view of cranium of *Melanocetus johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled, open spaces solid black.

distance between the tips of the sphenotic bones (Figures 1, 2) The head of the vomer, bearing as many as 10 recurved teeth, is also unusually wide (Figures 1, 2, 5-7). The frontals are triradiate in shape and widely separated from each other along their dorsal margins, approaching one another on the midline only at their ventromedial extensions. A semicircular-shaped pterosphenoid is present under the posterior extension of each frontal. The parasphenoid is well separated from the ventromedial extensions of the frontals. Posteromedially, the parasphenoid underlies the anterior

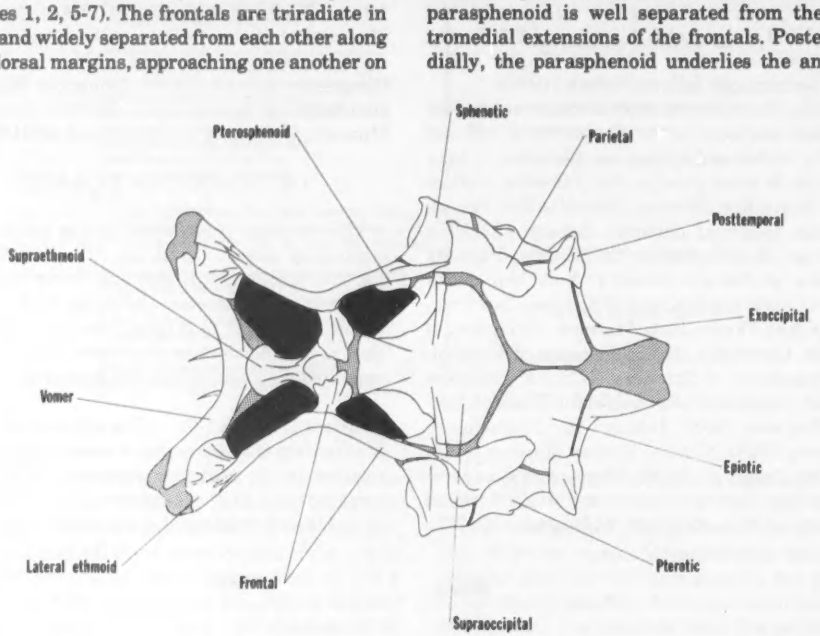

FIGURE 2.—Dorsal view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

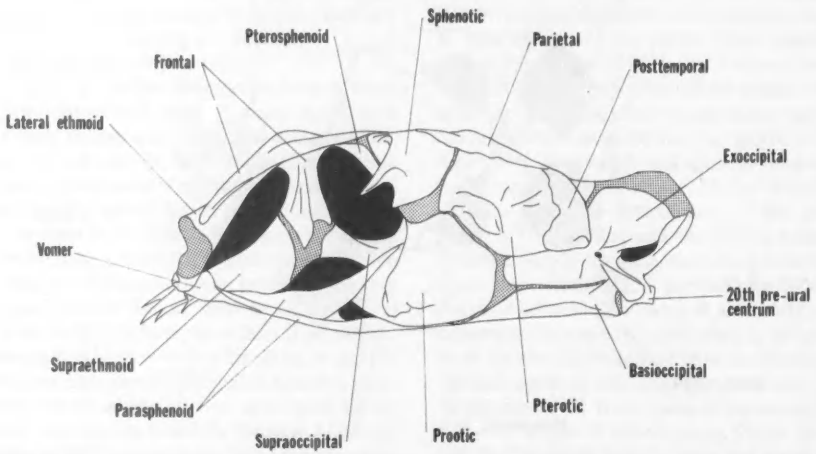

FIGURE 3.—Lateral view of cranium of *Melanocetus johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled, open spaces solid black.

projection of the supraoccipital; posteriorly directed dorsolateral extensions of the parasphenoid make contact laterally with the respective prootic (Figures 3, 4).

The large prootics are separated from each other anteriorly by the anterior process of the supraoccipital. Ventrally, each prootic forms a relatively large, anterolaterally directed, conical projection not found in other ceratioids (Figures 3-5, 8).

The supraoccipital is the largest element of the cranium, making up a considerable portion of the roof of the cranium. Together with the frontals, the supraoccipital forms the floor of a deep, V-shaped illicial trough (Figure 8). An anteriorly directed extension of the supraoccipital that sep-

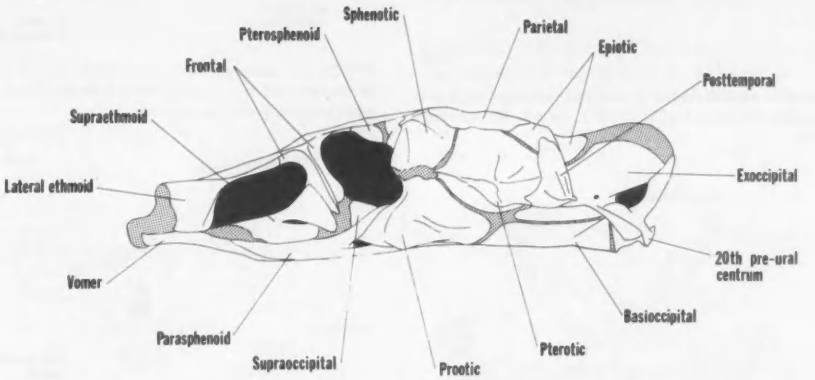

FIGURE 4.—Lateral view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

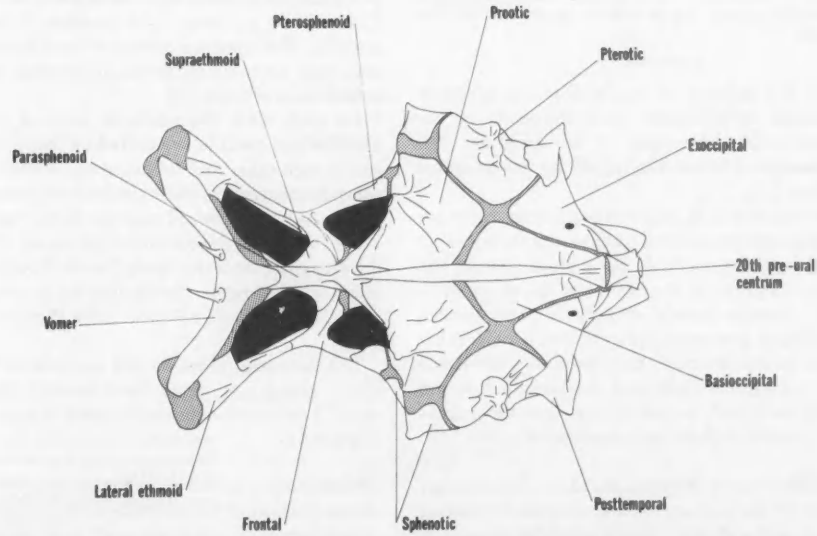

FIGURE 5.—Ventral view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

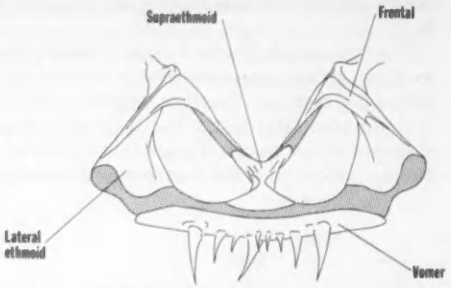

FIGURE 6.—Anterior view of anterior half of cranium of *Melanocetus johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled.

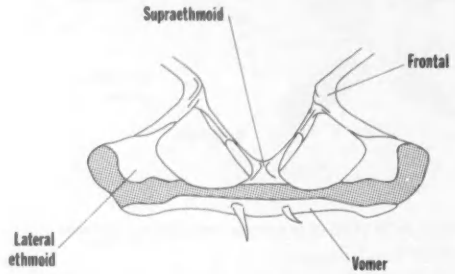

FIGURE 7.—Anterior view of anterior half of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled.

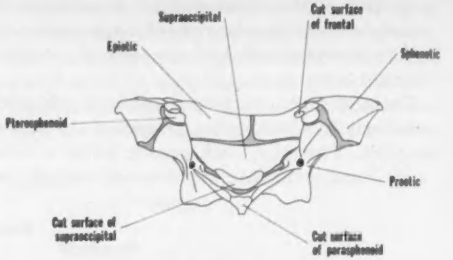

FIGURE 8.—Anterior view of posterior half of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL, anterior portion removed. Cartilage stippled.

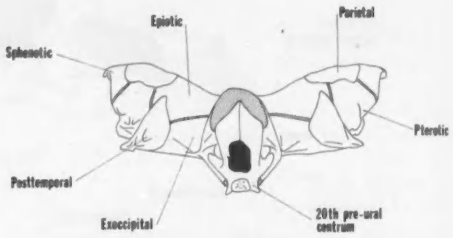

FIGURE 9.—Posterior view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled.

arates the prootics on the midline, is narrowly separated by cartilage from the ends of the ventromedial extensions of the frontals. The supraoccipital is not overlapped by the parietals (Figures 1-5).

The cranium of *M. murrayi* is considerably more elongate and compressed compared with that of its congeners (Figures 3, 4). As a consequence, the anterior margin of the vomer of *M. murrayi* is deeply concave (nearly straight in other forms), the frontals are more elongate and considerably lighter in construction, the sphenotics are much less produced forward, and the parietals do not extend posteriorly to overlap the posttemporals as they do in other *Melanocetus* species (Figures 1, 2).

Mandibular arch (Figures 10, 11).—The anterior portion of the premaxilla bears a short ascending process and a slightly longer articular process. A small (compared with those of oneirodids, Pietsch 1974) symphysial cartilage lies just behind the posteriorly notched symphysis of the premaxillae. There is no postmaxillary process of the premaxilla. The elongate portion of each premaxilla may bear up to 89 recurved, depressible teeth of mixed sizes (Figure 10).

On each side, the posterior ends of the premaxilla and maxilla are united by connective tissue to each other and to the lateral surface of the ascending process of the articular of the lower jaw, preventing any forward rotation of the upper jaw bones to close off the corners of the mouth. There is no elongate, anterior maxillomandibular ligament originating on the dentary as in oneirodids (labial cartilage of Le Danois 1964; Pietsch 1972a, 1974).

The dentaries meet on the midline to form a strong symphysial spine. Each dentary may bear up to 71 recurved, depressible teeth of mixed sizes (Figure 11).

Palatine and hyoid arches (Figures 11, 12). — The distal portion of the palatine arch (including the mesopterygoid, ectopterygoid, and palatine) is elongate and slender throughout (Figure 11). The small mesopterygoid is in contact with the metap-

terygoid. The suspensorium is unusually narrow and elongate (due largely to the extremely narrow and elongate quadrate), and directed obliquely backward. The posterior head of the hyomandibular is the larger of the two heads forming a broad articulation with the pterotic. The interhyal is short and relatively thick (compared with that of oneirodids, Pietsch 1974).

The hyoid apparatus (including epihyal, ceratohyal, and upper and lower hypohyals) is relatively short and thick (Figure 12). The lower hypohyal extends down beyond the ventral margin of the ceratohyal. In other ways this portion of the hyoid arch does not differ substantially from that described for oneirodids (Pietsch 1974).

Opercular apparatus (Figure 11). — The opercular apparatus is somewhat reduced (compared with that of oneirodids, Pietsch 1974). The opercle

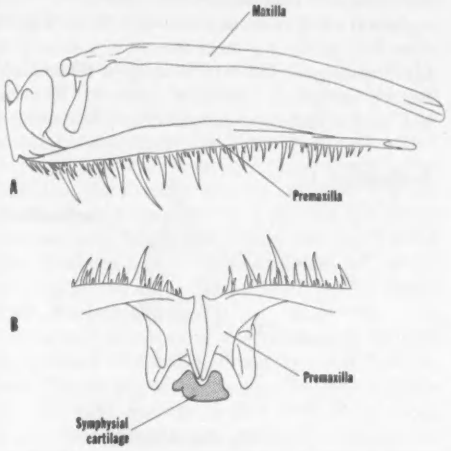

FIGURE 10.—Elements of upper jaw of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL: A. Maxilla and premaxilla, left lateral view; B. Symphysis of premaxillae, dorsal view.

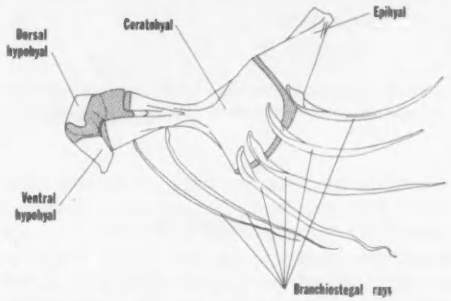

FIGURE 12.—Lateral view of hyoid apparatus of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL, interhyal not shown. Cartilage stippled.

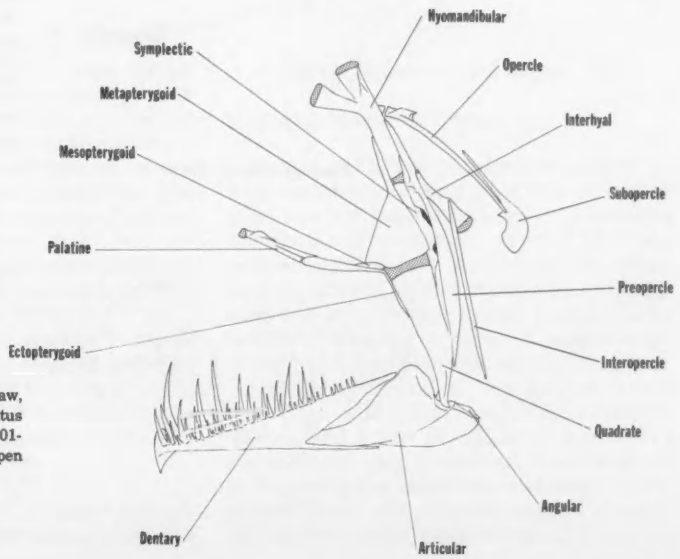

FIGURE 11.—Lateral view of lower jaw, suspensorium, and opercular apparatus of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

is notched posteriorly, but the upper fork of this bone is considerably shorter than the lower fork and sometimes absent. The subopercle is narrow and elongate, the upper part tapering to a fine point, the lower part rounded with a well-developed anterior spine or projection. The interopercle is unusually long and slender. The preopercle is more or less straight.

Branchial arches (Figure 13). — Pharyngobranchials I and IV are absent; those of the second and third arches are well developed, bearing four to nine recurved and depressible fangs. Epibranchial I is reduced lying free in the connective tissue matrix. Ceratobranchial V is also reduced but tightly connected to the medial-proximal margin of ceratobranchial IV. There are three hypobranchials, and a single basibranchial ossification surrounded by a triangular-shaped cartilage.

Vertebrae and caudal skeleton (Figure 14).—The vertebral column forms a sigmoid curve, dipping down behind the region of the gut and sloping up again to support the tail. In the five cleared and stained specimens examined there are 20 vertebral centra (including the half-centrum to which is

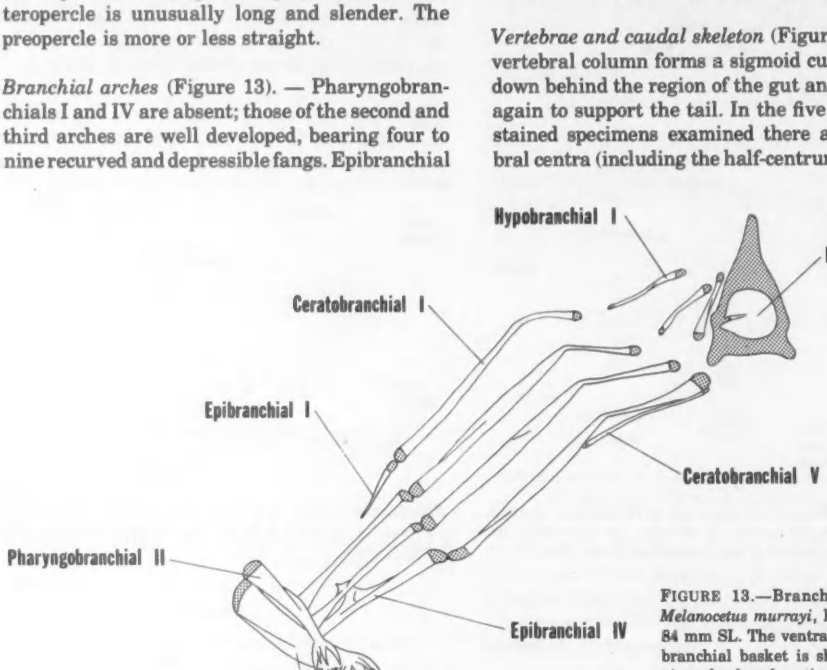

FIGURE 13.—Branchial arches of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view. Cartilage stippled.

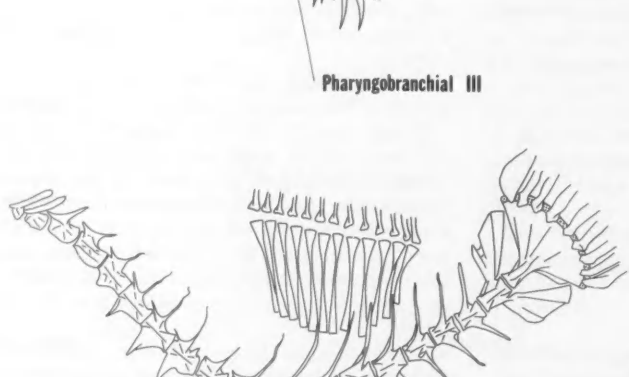

FIGURE 14.—Lateral view of vertebral column, dorsal and anal fins, and caudal skeleton of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled.

fused the hypural plate, Pietsch 1972a) of which 13-15 are caudal vertebrae (those bearing complete haemal arches). Epurals are absent. The hypural plate is unnotched posteriorly and bears the overlapping bases of nine principal caudal rays, the uppermost of which is exceptionally large. The uppermost and two lowermost caudal rays are simple, the central rays are bifurcated distally.

Median fins and illicial apparatus (Figures 14, 15). — There are 13-19 biserial, segmented, and unbranched dorsal fin rays, the number varying somewhat among species. The rays are supported by elongate, closely associated radials, usually one less than the number of rays. All species of the genus have 4 anal fin rays (of 353 specimens counted, only 2 had 3 anal rays, and only 2 had 5 rays) that are like those of the dorsal fin, invariably supported by 3 similar, closely associated radials (Table 2, Figure 14).

The pterygiophore of the illicium is strongly compressed with a thin, bladelike ventral expansion. The length of the pterygiophore varies from 17% SL in *M. murrayi* to 33% SL in *M. johnsoni*. The remnant of the second cephalic ray is a minute ossification lying on the pterygiophore just behind the articulation with the illicial bone (Figure 15). The length of the illicial bone varies slightly among *Melanocetus* species, becoming longer proportionately with growth.

Pectoral girdle, pectoral fin, and pelvic bone (Figure 16).—Each posttemporal overlaps the respective pterotic, epiotic, and exoccipital. It is in turn overlapped by the parietal in *M. johnsoni*, but widely separated from this bone in *M. murrayi*.

An ossified posteroventral process of the coracoid is absent but perhaps represented by a posteroventral cartilaginous extension. There are four pectoral radials, the lower two of which become completely fused with each other giving the appearance of only three radials (Regan and Trewavas 1932, fig. 22; Pietsch 1972a).

The pectoral fin lobe of *M. murrayi* is considerably smaller than that of other *Melanocetus* species (Figure 16A). In other ways the elements of the pectoral girdle, pectoral fin, and pelvic bone do not differ substantially from those of oneirodids (Pietsch 1974).

Skin spines.—Minute dermal spines (approximately 0.03-0.11 mm long) are present in the skin

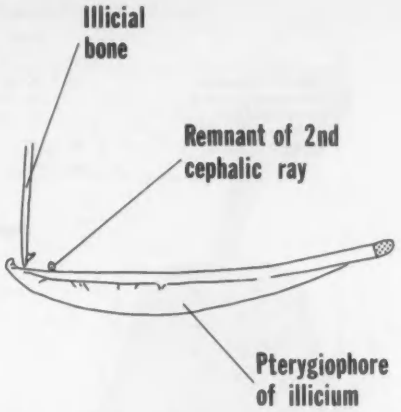

FIGURE 15.—Bones of illicial apparatus of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL, left lateral view. Cartilage stippled.

of the two species examined osteologically. In *M. johnsoni* they are most numerous on the side of the trunk under the dorsal fin (where there are about 6 spines/mm^2)but become progressively more widely scattered anteriorly and finally disappear in the area of the upper and lower jaws (Struhsaker 1962). In the two specimens of *M. murrayi* examined osteologically the spines are confined to the caudal peduncle.

SYSTEMATICS

Family Melanocetidae Regan 1912

Type genus *Melanocetus* Günther 1864

Diagnosis. — The metamorphosed females of the Melanocetidae are distinguished from those of all other ceratioid families by having the following combination of characters: jaws equal anteriorly; supraethmoid present; parietals present; pterosphenoid present; anterior maxillomandibular ligament absent (Pietsch 1972a); hyomandibular with a double head; hypohyals 2; branchiostegal rays 6; operculum bifurcate, upper fork reduced; suboperculum slender, as long as lower fork of operculum, with strong anterior spine; pharyngobranchials I and IV absent; epibranchial I reduced; a single ossified basibranchial; epibranchial and ceratobranchial teeth absent; epurals absent; only an ossified remnant of second cephalic ray present; dorsal fin rays 13-17, anal fin

TABLE 2.—Fin ray frequencies for females of *Melanocetus* species.

Species	Dorsal						Anal			Pectoral (both sides)							
	12	13	14	15	16	17	3	4	5	15	16	17	18	19	20	21	22	23
Melanocetus johnsoni		6	70	64	2	1	1	136	1			13	34	69	36	12	2	1
Melanocetus polyactis			4	4	4	2		13	1			2	3	12	4	2	1	
Melanocetus niger			3	2				5					2	2	5	1		
Melanocetus eustalus				1				1			2							
Melanocetus murrayi	1	32	29					62		5	17	37	8	5	1			
Total	1	38	106	71	6	3	1	217	2	5	19	52	47	86	46	15	3	1

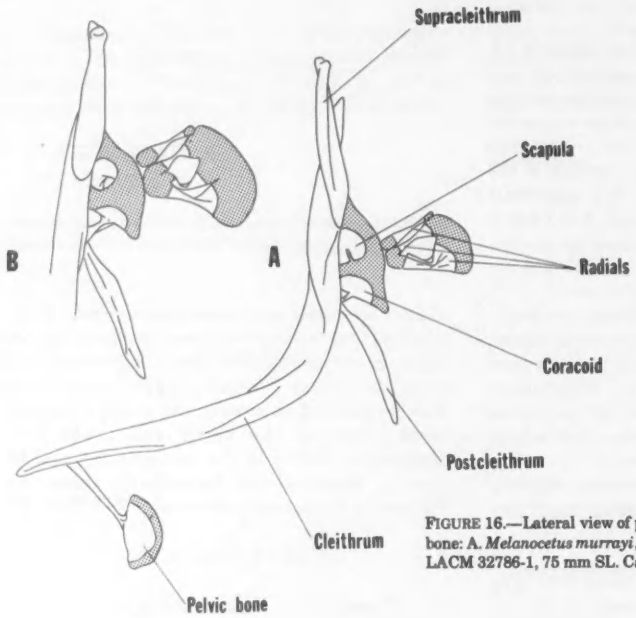

FIGURE 16.—Lateral view of pectoral girdle, pectoral radials, and pelvic bone: A. *Melanocetus murrayi*, LACM 31501-3, 84 mm SL; B. *M. johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled.

rays 4 (rarely 3 or 5), caudal fin rays 9 (1-6-2); ossified posteroventral process of coracoid absent; pectoral radials 4, fusing to 3 with growth; pelvic bones expanded distally; esca without denticles; minute, widely spaced skin spines present in at least some species.

The metamorphosed males of the Melanocetidae are distinguished from those of all other ceratioid families in having the following combination of characters: free-living; jaw teeth absent; upper denticular with 2-3 semicircular series of strong, recurved denticles, fused with a median series of 3-9 enlarged dermal spines that articulate with the pterygiophore of the illicium; lower denticular with 10-23 recurved denticles, fused into a median and two lateral groups; eyes directed laterally, elliptical in shape, pupil larger than lens; olfactory organs large, nostrils lateral, nasal area unpigmented, inflated; dorsal fin rays 12-16, anal fin rays 4, caudal fin rays 9 (1-6-2); skin spinulose or naked.

Description. — Females relatively short and deep, globular (but often appearing highly compressed apparently due to deformation upon capture, compare Figures 17, 18); head short; mouth large, nearly vertical, cleft not extending past eye; lower jaw with a well-developed symphysial spine; oral valve weakly developed; two nostrils on each side on distal surface of a rounded papilla; eye small, subcutaneous, appearing through a circular, translucent area of integument within a shallow, orbital pit formed between sphenotic and frontal bones; gill opening oval in shape, situated posteri-

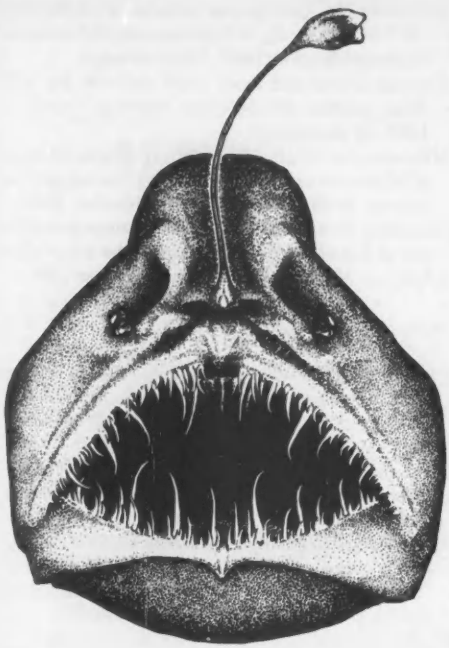

FIGURE 17.—Anterior view of *Melanocetus johnsoni*, LACM 31484-1, 85 mm SL. Drawn by Elizabeth Anne Hoxie.

or to pectoral lobe; all four epibranchials closely bound together by connective tissue; anterior half of ceratobranchial I bound to medial surface of ceratohyal by connective tissue, posterior half free; gill filaments present on anteriormost tip of ceratobranchial I and full length of ceratobranchials II through IV; pseudobranch absent; no opening behind fourth gill arch; ovaries paired; pyloric caeca absent.

Illicial length 23.1-60.8% SL; anteriormost tip of pterygiophore of illicium exposed, emerging on snout between eyes, its posterior end concealed under skin; escal bulb simple, usually with a rounded or conical, distal prolongation, and often with posterior and anterior crests; elongate appendages and filaments absent.

Jaw teeth slender, recurved, and depressible, some slightly hooked distally, those in lower jaw less numerous, but slightly longer than those in upper jaw; number of teeth in lower jaw 32-142, in upper jaw 29-178; longest tooth in lower jaw 6.9-

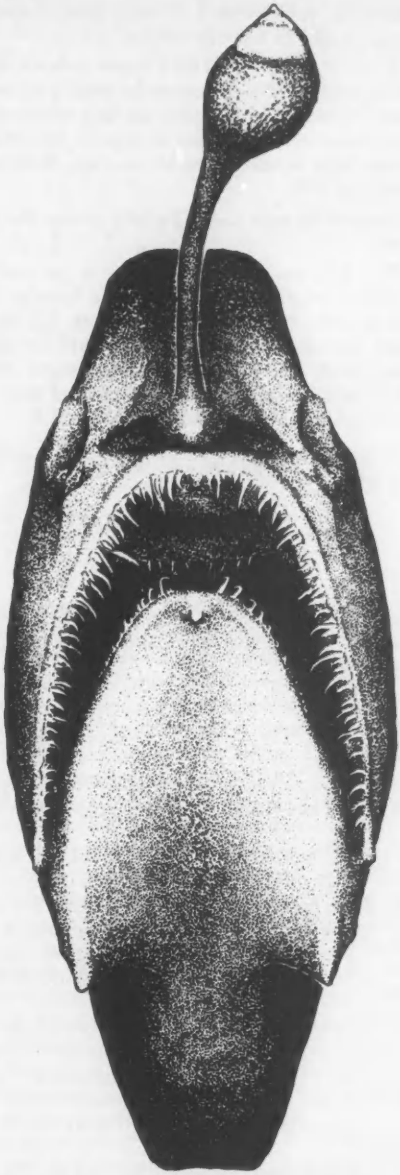

FIGURE 18.—Holotype of *Melanocetus eustalus*, LACM 30037-12, 111 mm SL, anterior view. Drawn by Elizabeth Anne Hoxie.

25.0% SL; vomer with 0-12 teeth; pharyngobranchials II and III heavily toothed.

Color in preservative dark brown to black over entire surface of body (except for distal portion of escal bulb) and oral cavity; all fins colorless in specimens less than about 40 mm SL (except for caudal rays in adolescent *M. murrayi*, Bertelsen 1951, fig. 16I).

Pectoral fin rays 15-23 (Table 2); pelvic fins absent.

The following measurements, in percent of standard length, are summarized for females (20-120 mm SL) of all species: head depth 42.5-82.0; least outside width between frontals 9.1-28.6; head width 22.6-45.0; premaxillary length 36.3-76.0; lower jaw length 36.7-78.0; width of pectoral fin lobe 6.1-17.8; escal bulb width 1.9-11.3

For description of males see Diagnosis above and Bertelsen (1951).

Genus *Melanocetus* Günther 1864

Females

Melanocetus Günther 1864:301-302, pl. 25 (type species *Melanocetus johnsoni* Günther 1864, by monotypy).

Melanocetus (subgenus *Liocetus*) Günther 1887:56, pl. 11, fig. A (type species *Melanocetus murrayi* Günther 1887, by monotypy).

Liocetus Goode and Bean 1896: 495-496, fig. 407 (type species *Melanocetus murrayi* Günther 1887, by monotypy).

Melanocoetus Smith 1949:429 (erroneous spelling of *Melanocetus*, therefore taking the same type species, *Melanocetus johnsoni* Günther 1864).

Linocetus Bertelsen 1951:40, 44 (erroneous spelling of *Liocetus*, therefore taking the same type species, *Melanocetus murrayi* Günther 1887).

Males

Rhynchoceratias Parr 1927:30-33, fig. 11-12 (in part; type species *Rhynchoceratias brevirostris* Regan 1925, by subsequent designation of Fowler 1936).

Centrocetus Regan and Trewavas 1932:53, fig. 79 (type species *Centrocetus spinulosus* Regan and Trewavas 1932, by monotypy).

Xenoceratias Regan and Trewavas 1932:54-57, fig. 80-84 (type species *Xenoceratias longirostris* Regan and Trewavas 1932, by subsequent designation of Fowler 1936).

Diagnosis and description same as for family.

Key to Species Based on Females

The following key will differentiate female specimens >20 mm SL (for males and larvae see Bertelsen 1951). The key should be used in conjunction with Figures 19-24.

1A. Escal bulb width 11.3% SL in 111 mm specimen (Figures 18, 28); longest lower jaw tooth 5.9% SL in 111 mm specimen ..... *Melanocetus eustalus* n. sp. (single known female)

1B. Escal bulb width <10% SL (Figure 17); longest lower jaw tooth 6.9-25.0% SL 2

2A. Anterior margin of vomer deeply concave (Figure 2); least outside width between frontals 9.1-17.8% SL (Figure 19); number of lower jaw teeth 46-142 (>60 in specimens 25 mm and larger) (Figure 20); escal bulb width 1.9-5.1% SL (<3% SL in specimens >50 mm SL) ..... *Melanocetus murrayi* Günther 1887

2B. Anterior margin of vomer nearly straight (Figure 1); least outside width between frontals 13.5-28.6% SL (Figure 19); number of lower jaw teeth 32-90 (Figure 20); escal bulb width 3.8-8.6% SL (>4% SL in specimens >50 mm SL) 3

3A. Longest lower jaw tooth 8.4-25.0% SL (Figure 21); esca with compressed posterior and (usually) anterior crests (Figure 25); distribution nearly cosmopolitan ..... *Melanocetus johnsoni* Günther 1864

3B. Longest lower jaw tooth 6.9-13.1% SL (Figure 21); esca without posterior or anterior crests (Figures 26, 27); distribution restricted to eastern tropical Pacific 4

4A. Number of lower jaw teeth 58-90 (Figure 22); escal bulb width 5.2-8.5% SL (Figure 23); illicium length 34.6-56.0% SL (Figure 24); escal bulb with a conical, distal prolongation occasionally pigmented on tip (Figure 26) ..... *Melanocetus polyactis* Regan 1925

4B. Number of lower jaw teeth 37-57 (Figure 22); escal bulb width 3.8-5.0% SL (Figure 23); illicium length 29.8-38.8% SL (Figure 24); escal bulb with a low, rounded distal prolongation usually darkly pigmented on tip (Figure 27) ..... *Melanocetus niger* Regan 1925

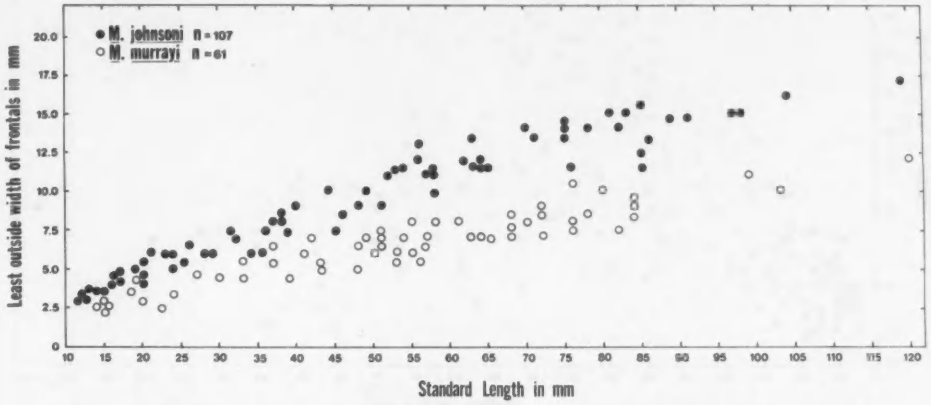

FIGURE 19.—Relationship between least outside width of frontals and standard length for two species of *Melanocetus*.

Melanocetus johnsoni Günther 1864
Figures 1, 3, 6, 16B, 17, 19-21, 25, 30, 31

Females

Melanocetus johnsoni Günther 1864:301-303, pl. 25 (original description, single specimen, holotype BMNH 1864.7.18.6, 64 mm, Madeira, 24 December 1863); Lütken 1871:64, 74 (comparison with *Oneirodes eschrichtii*); Lütken 1872:329-340, 343 (after Lütken 1871); Günther 1880:473, fig. 211 (after Günther 1864); Günther 1887:56-57 (after Günther 1864, comparison with *M. murrayi*); Vaillant 1888:346 (after Günther 1864); Goode and Bean 1896:494, fig. 406 (description after Günther 1864); Gill 1909:582, 584, 585, fig. 20 (after Günther 1864, Goode and Bean 1896); Regan 1912:286, fig. 6C (cranial osteology); Regan 1913:1096 (description of additional specimen, natural history); Regan 1926:18, 32, 33, fig. 10 (description of additional material, cranial osteology; *M. krechi* and *M. rotundatus* synonyms); Parr 1927:29 (description of additional specimen); Norman 1930:354 (additional record); Regan and Trewavas 1932:27-29, 49-52, fig. 19-21, 22A, B, 72, 73 (description of additional material, osteology, and esca figured, in key); Fowler 1936:1143, 1144, 1346, 1363 (description after Günther 1864, Regan 1926, Norman 1930); Norman 1939:114 (additional material); Koefoed 1944:3-5, pl. 1, fig. 1 (description of additional specimen, comparison with *M. murrayi*; Beebe and Crane 1947:152 (description of additional specimen, color); Fowler 1949:158-159 (listed); Bertelsen 1951:7, 40-41, 43-46, 48-53, fig. 13, 15, 17-19, tables 4, 6 (description of females, males, larvae, comparison with all known material, in key); Grey 1956:235-236 (synonymy; distribution); Monod 1960:687, fig. 80 (pectoral radials); Maul 1961:91-92, fig. 1 (description of additional material); Maul 1962a:6-7 (description, additional material); Struhsaker 1962:841-842 (description, additional specimen, skin spines); Bussing 1965:222 (additional specimen); Fitch and Lavenberg 1968:127, fig. 70 (distinguishing characters, natural history); Pietsch 1972a:29, 35, 36, 38, 45 (osteological comments); Maul 1973:667 (synonymy, after Bertelsen 1951).

Melanocetus krechi Brauer 1902:293-294 (original description, single specimen, holotype ZMHU 17688, 45 mm, *Valdivia* stn. 239, Indian Ocean, 5°42′ S, 43°36′ E, 0-2,500 m); Brauer 1906:319-320, pl. 15, fig. 1, 2 (description after Brauer 1902); Gill 1909:583, 584, fig. 21 (after Brauer

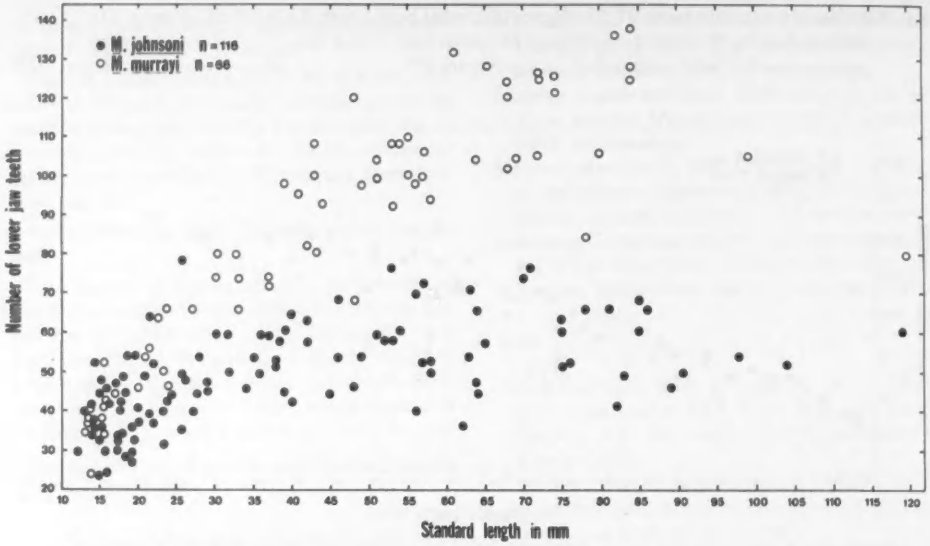

FIGURE 20.—Relationship between number of lower jaw teeth and standard length for two species of *Melanocetus*.

1902, 1906); Murray and Hjort 1912:87, 614 (in part, additional specimen, misidentification); Borodin 1931:84 (additional specimen, misidentification); Regan and Trewavas 1932:49, 52, fig. 74 (misidentification, in key); Fowler 1936: 1143, 1144 (description after Brauer 1902, 1906, in key); Bertelsen 1951:40, table 4 (comparison with all known material).

Melanocetus rotundatus Gilchrist 1903:206-208, pl. 15 (original description, two specimens, both lost [see Comments, p. 76], the largest about 28 mm, off Cape Point and Natal coast, South Africa, 1,098 m); Gilchrist and Thompson 1917:417 (after Gilchrist 1903); Barnard 1927:1007, pl. 37, fig. 5 (after Gilchrist 1903); Bertelsen 1951:48 (in synonymy of *M. johnsoni*).

Melanocoetus rotundatus, Smith 1949:429, fig. 1232 (after Gilchrist 1903); Penrith 1967:187, 188 (type material lost; a synonym of *M. johnsoni*).

Melanocetus ferox Regan 1926:33, pl. 9, fig. 1 (original description, single specimen, holotype ZMUC P9257, 78 mm, *Dana* stn. 1208(14), Gulf of Panama, 6°48′ N, 80°33′ W, 3,100 m wire, 1715 h, 16 January 1922); Regan and Trewavas 1932:49, 52, fig. 75 (in part, only holotype, additional material here referred to *M. polyactis*, in key); Beebe and Crane 1947:152 (in part, only holotype); Bertelsen 1951:44, 53, table 4 (in part, only holotype; comparison with all known material, in key); Grey 1956:237 (synonymy, distribution).

Melanocetus cirrifer Regan and Trewavas 1932:52-53, fig. 76A, 77, pl. 2, fig. 1 (original description, two females, lectotype ZMUC P9258, 25.5 mm, *Dana* stn. 3678(2), Banda Sea, 4°05′ S, 128°16′ E, 4,000 m wire, bottom depth 4,700 m, 1840 h, 24 March 1929, in key); Bertelsen 1951:44, 53, table 4 (description, comparison with all known material, in key); Grey 1956:237 (synonymy, distribution).

Melanocetus niger, Gregory 1933:400, fig. 272 (misidentification, osteology).

Melanocetus megalodontis Beebe and Crane 1947:152, fig. 1 (original description, single specimen, holotype CAS-SU 46488 [originally NYZS 25791], 25.5 mm, Templeton Crocker Expedition stn. 165 T-3, eastern tropical Pacific, 20°36′ N, 115°07′ W, 0-915 m, 17 May 1936); Bertelsen 1951:43, 48, table 4 (description, comparison with all known material, in key); Grey 1956:235 (synonymy, distribution); Mead 1958:133 (holotype passed to CAS).

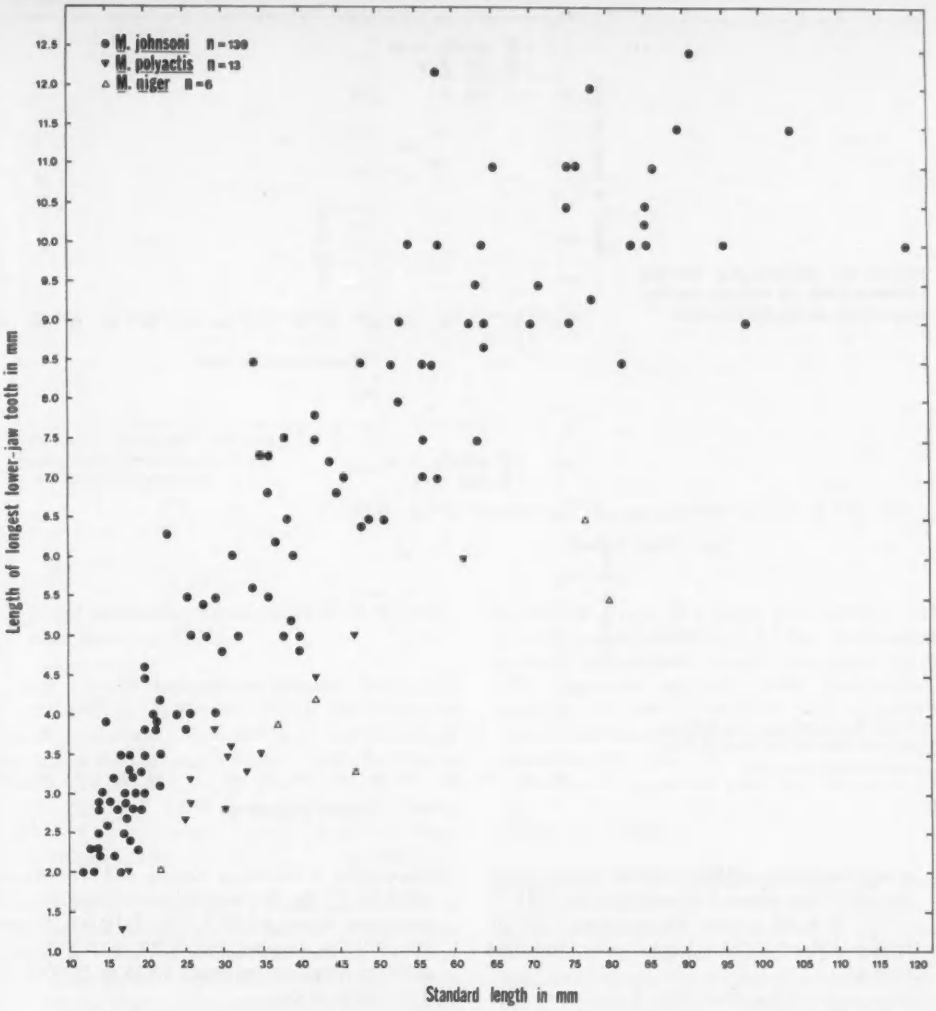

FIGURE 21.—Relationship between length of longest lower jaw tooth and standard length for three species of *Melanocetus*.

Melanocetus sp. Roule and Angel 1930:121, pl. 6, fig. 159 (additional material).

Males

Centrocetus spinulosus Regan and Trewavas 1932:53, 54, fig. 79 (original description, two specimens, lectotype ZMUC P9246, 15.5 mm, *Dana* stn. 3847(2), Indian Ocean, 12°02′ S, 96°43′ E, 3,000 m wire, bottom depth 2,825 m, 2100 h, 11 October 1929).

Xenoceratias macracanthus Regan and Trewavas 1932:11, 12 (erroneous spelling of specific name, listed).

Xenoceratias micracanthus Regan and Trewavas 1932:54, 55, fig. 81 (original description, single

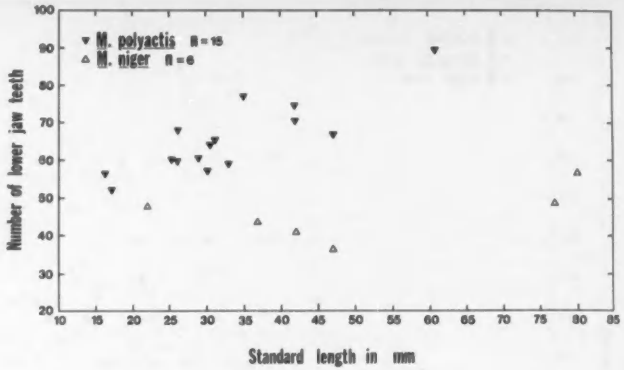

FIGURE 22.—Relationship between number of lower jaw teeth and standard length in two species of *Melanocetus*.

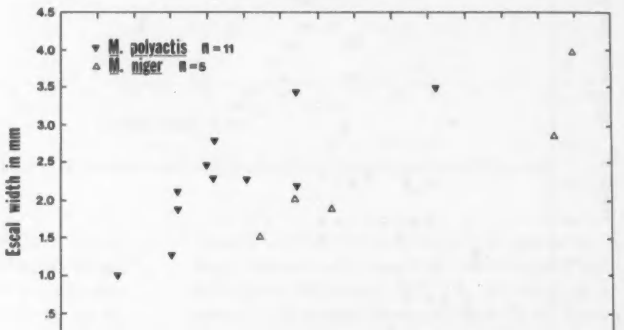

FIGURE 23.—Relationship between escal bulb width and standard length in two species of *Melanocetus*.

specimen, holotype ZMUC P9250, 28 mm, *Dana* stn. 4000(8), eastern tropical Atlantic, 0°31′ S, 11°02′ W, 4,000 m wire, bottom depth 3,750 m, 0630 h, 4 March 1930, in key); Fowler 1936:1364 (listed).

Xenoceratias heterorhynchus Regan and Trewavas 1932:54, 56, fig. 82 (original description, single specimen, holotype ZMUC P9248, 27 mm, *Dana* stn. 3716(2), South China Sea, 19°18.5′ N, 120°13′ E, 3,000 m wire, bottom depth 3,225 m, 1400 h, 22 May 1929, in key); Grey 1956:236 (synonymy, distribution).

Xenoceratias laevis Regan and Trewavas 1932:54, 57, fig. 83 (original description, single specimen, holotype ZMUC P9249, 23 mm, *Dana* stn. 3731(13), South China Sea, 14°37′ N, 119°52′ E, 2,000 m wire, bottom depth 2,300 m, 0200 h, 17 June 1929, in key).

Xenoceratias brevirostris Regan and Trewavas 1932:54, 57, fig. 84 (original description, single specimen, holotype ZMUC P9247, 19 mm, *Dana* stn. 3739(8), Celebes Sea, 3°20′ N, 123°50′ E, 3,000 m wire, bottom depth 4,475 m, 0700 h, 2 July 1929, in key).

Xenoceratias braueri Koefoed 1944:6, fig. 2 (original description, single specimen, holotype UBZM 4309, 18.5 mm, *Michael Sars* North Atlantic Deep-Sea Expedition stn. 53, central North Atlantic, 34°59′ N, 33°01′ W, 2,600 m wire, bottom depth 2,615-2,865 m, 8-9 June 1910).

Melanocetus johnsoni, Bertelsen 1951:44, 48-53, fig. 17C, D, F-H, table 6 (synonymy, distribution, comparison with all known material, in key); Grey 1956:236 (synonymy, distribution); Maul 1962b:36-37, fig. 2 (description of addi-

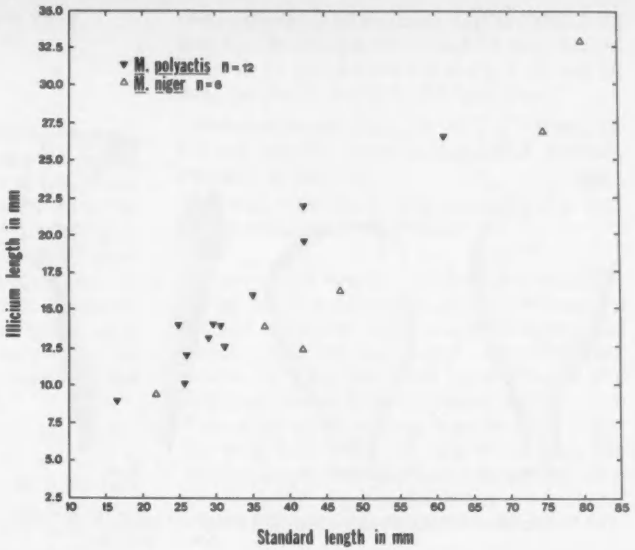

FIGURE 24.—Relationship between illicium length and standard length in two species of *Melanocetus*.

tional specimen); Maul 1973:667 (synonymy, after Bertelsen 1951).

Material. — Metamorphosed females, 346 (10-119 mm): AMS, 33 (11-88 mm); BMNH, 16 (13-64 mm); CAS, 1 (25.5 mm); FSM, 10 (13-76 mm); IOAN, 35 (12-75 mm); IOS, 7 (35-91 mm); ISH, 82 (15-119 mm); LACM, 65 (13.5-83 mm); MCZ, 25 (12-75 mm); NMNZ, 7 (12-55 mm); ROM, 4 (15-56 mm); SAM, 6 (10-13 mm); UMML, 3 (27-82 mm); USNM, 15 (12-85 mm); ZMUC, 37 (11.5-89 mm).

Diagnosis.—A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight (Figure 1); least outside width between frontals 13.5-28.6% SL (Figure 19); number of lower jaw teeth 32-78 (Figure 20), length of longest lower jaw tooth 8.4-25.0% SL (Figure 21); width of pectoral fin lobe 10.7-17.8% SL; escal bulb width 4.3-8.6% SL; illicium length 32.4-60.8% SL; esca with posterior and (usually) anterior crests (Figure 25); minute skin spines present over most of body; integument relatively thick (1.55 mm).

Description.—Escal bulb slightly compressed with a low, rounded or conical distal prolongation nearly always darkly pigmented on tip; a compressed posterior crest usually darkly pigmented, becoming larger and more conspicuous with growth; and a considerably smaller, compressed, anterior crest present in some specimens (Figure 25); integument relatively thick (cross sections measure 1.55 mm in thickness), not easily torn, usually retaining heavy pigmentation during fixation and preservation.

Number of upper jaw teeth 48-134; dorsal fin rays 13-15 (rarely 16), pectoral fin rays 17-22 (rarely 23) (Table 2).

Distribution. — *Melanocetus johnsoni* has a wide horizontal distribution in tropical and subtropical waters of all three major oceans of the world (see Distribution, p. 83). Compared with *M. murrayi*, it appears to occupy relatively shallow depths: about 62% of the material (for which data was available) was captured by open nets fished at maximum depths of 1,000 m; 82% of the material can be accounted for by gear fished above 1,500 m, and 98% by gear fished above 2,100 m (see Distribution, p. 83).

Comments. — *Melanocetus krechi* Brauer (1902) was synonymized with *M. johnsoni* by Regan (1926), resurrected by Regan and Trewavas (1932), and tentatively synonymized again with *M. johnsoni* by Bertelsen (1951). From the description and figure given by Brauer (1902, 1906)

FIGURE 25.—Escae of *Melanocetus johnsoni*: A. ISH 1261/71, 21 mm SL; B. ISH 753/71, 38 mm SL; C. MCZ 49849, 75 mm SL; D. ISH 1534/71, 78 mm SL.

and based on a much greater knowledge of variation within the genus, there can be little doubt that this nominal form has been correctly placed within the synonymy of *M. johnsoni*.

Melanocetus ferox was described from a single specimen (78 mm) collected in the Gulf of Panama (Regan 1926). Two additional specimens of this nominal form were listed by Regan and Trewavas (1932). A thorough comparison of all known material led Bertelsen (1951, table 4) to suspect that *M. ferox* might represent individual variation of *M. niger*. The holotype of *M. ferox*, however, has relatively long lower jaw teeth (longest, 12.0% SL; Figure 21). In this, and in all other morphometric and meristic characters used here, it fits well within the material here recognized as *M. johnsoni*. Although the esca of the holotype is in poor condition, traces of a posterior crest remain. For these reasons *M. ferox* is synonymized with *M. johnsoni*. The two additional specimens identified as *M. ferox* by Regan and Trewavas (1932) (ZMUC P92210, 30.5 mm; BMNH 1932.5.3.6, 42 mm) have short jaw teeth; in this and in other ways they fit well within the material of *M. polyactis* (see p. 77).

Melanocetus cirrifer Regan and Trewavas (1932), described on the basis of two small females, was tentatively maintained by Bertelsen (1951) because of supposed differences in escal morphology and pigmentation which now can easily be shown to be part of the variation found within *M. johnsoni*. *Melanocetus megalodontis* Beebe and Crane (1947), based on a single specimen, was distinguished from all other species of the genus by ". . . the character of the illicium; in the great length and robustness of the fangs . . . and in the shortness of the lower jaw. . . ." However, specimens of *M. johnsoni* may have longer teeth and individuals of several species of *Melanocetus* may have as short a lower jaw (Bertelsen 1951, table 4). Further (as predicted by Bertelsen 1951), the "peculiar minute distal flaps" of the esca are artifacts. In all ways the holotype of *M. megalodontis* fits well within the variation now known to occur within *M. johnsoni*. Thus these nominal forms, *M. cirrifer* and *M. megalodontis*, are placed within the synonymy of *M. johnsoni*.

Finally, the holotype and paratype of *M. rotundatus* Gilchrist (1903) have been lost. The circumstances of their demise are the same as for the holotype of *Dolopichthys cornutus* described elsewhere (Pietsch 1972b; see also Barnard 1927, Penrith 1967). Although Gilchrist's (1903) original description is poor, the figure provided by him shows rather long jaw teeth, a long illicium bearing a relatively large escal bulb, and a large pectoral fin lobe. This combination of characters makes it nearly certain that *M. rotundatus* is a synonym of *M. johnsoni* (Penrith 1967).

Melanocetus polyactis Regan 1925
Figures 21-24, 26, 30

Females

Melanocetus polyactis Regan 1925:565 (original description, 3 specimens, lectotype designated by Bertelsen 1951, ZMUC P9260, 61 mm, *Dana* stn. 1206(3), Gulf of Panama, 6°40′ N, 80°47′ W, 3,500 m wire, 1845 h, 14 January 1922); Regan 1926:34, pl. 8, fig. 2 (description after Regan 1925); Regan and Trewavas 1932:53, fig. 78 (listed, after Regan 1925, 1926); Bertelsen 1951:44, 54-55, tables 4, 7, 8 (description, additional material, 2 males, 6 larvae, comparison with all known material, in key); Grey 1956:238 (synonymy, distribution).

Melanocetus niger Regan 1925:565 (in part, 3 of 11 cotypes [see Comments, p. 79], all Gulf of Panama); Regan 1926:33, pl. 8, fig. 1 (in part, description, 4 additional specimens); Regan and Trewavas 1932:53, fig. 76B (in part, listed, after Regan 1925, 1926); Bertelsen 1951:44, 53, table 4 (in part, description, comparison with all known material, in key); Grey 1956:237 (in part, synonymy, distribution).

Melanocetus ferox, Regan and Trewavas 1932:49, 52, fig. 75 (in part, nontype material only, in key); Bertelsen 1951:44, 53, table 4 (in part, nontype material only, comparison with all known material, in key); Grey 1956:237 (in part, after Bertelsen 1951, synonymy, distribution).

Males

Rhynchoceratias rostratus, Regan 1926:44 (in part, misidentification).

Rhynchoceratias leucorhinus, Regan 1926:44 (in part, misidentification).

Material. — Metamorphosed females, 15 (16.5-61 mm): BMNH 1925.8.11.30, 26 mm; BMNH 1925.8.11.32, 42 mm (paralectotype); BMNH 1932.5.3.6, 42 mm; IOAN uncatalogued, 33 mm; LACM 33603-4, 2 (16.5 and 30 mm); LACM 33574-5, 17 mm; LACM 33624-1, 33 mm; LACM 33629-3, 35 mm; ZMUC P92155, 25 mm (paralectotype); ZMUC P921974, 26 mm; ZMUC P9251, 29 mm; ZMUC P92210, 30.5 mm; ZMUC P9253, 47 mm; ZMUC P9260, 61 mm (lectotype).

The following adolescent females, all collected from the eastern tropical Pacific, are only tentatively referred to *M. polyactis*: LACM 33618-2, 16 mm; LACM 31119-2, 2 (17 and 18 mm); LACM 31109-2, 18 mm; LACM 31120-20, 2 (18 and 19 mm); LACM 31126-29, 2 (19.5 and 20 mm).

Metamorphosed males, 2: ZMUC P92460, 16 mm (22 mm total length (TL)); ZMUC P92459, 19.5 mm (30 mm TL).

Larvae, 6 (2 males, 4 females, 3-9 mm TL): ZMUC P92461; ZMUC P92462.

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight; least outside width between frontals 18.0-26.0% SL; number of lower jaw teeth 58-90 (Figure 22); length of longest lower jaw tooth 9.3-13.1% SL (Figure 21); width of pectoral fin lobe 10.9-16.0% SL; escal bulb width 5.2-8.5% SL (Figure 23); illicium length 34.6-56.0% SL (Figure 24); esca with a conical, distal prolongation, crests absent (Figure 26); integument relatively thick.

Description. — Escal bulb not compressed, with conical distal prolongation nearly always slightly constricted at base, and usually as long as or longer than length of escal bulb, pigmented on tip in some specimens, posterior and anterior crests absent (Figure 26); integument as in *M. johnsoni*.

Number of upper jaw teeth 42-120; dorsal fin rays 14-17; pectoral fin rays 17-21 (rarely 22 and 23) (Table 2).

Distribution. — *Melanocetus polyactis* appears to be restricted to the eastern tropical Pacific Ocean where 15 specimens have been collected between lat. 10° N and 13° S as far west as long. 88° W (see Distribution, p. 83). Approximately 67% of the material was captured by open nets fished at maximum depths of 1,000 m or below.

Comments. — *Melanocetus polyactis* is most easily confused with *M. niger*. Both forms are similar in having exceptionally short lower jaw teeth (Figure 21). They differ significantly, however, in the number of lower jaw teeth, escal bulb width, and illicial length (see Key, Figures 22-24).

Part of the material originally listed as *M. niger* has been reallocated to *M. polyactis* (see Comments, p. 79). Also included with the material of *M. polyactis* are two specimens (ZMUC P92210, 30.5 mm; BMNH 1932.5.3.6, 42 mm) previously identified as *M. ferox* by Regan and Trewavas (1932).

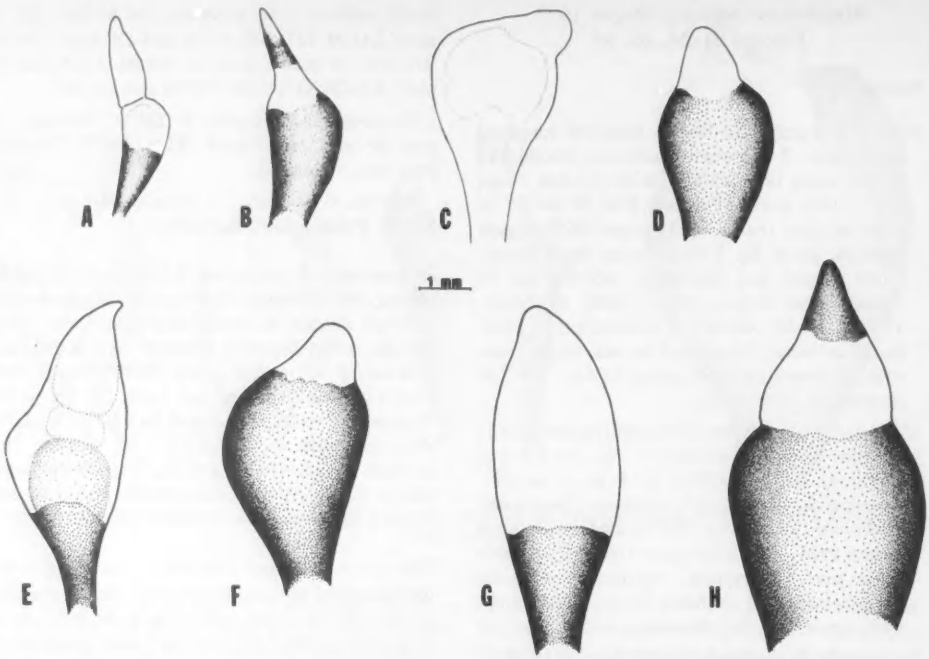

FIGURE 26.—Escae of *Melanocetus polyactis*: A. LACM 33603-4, 16.5 mm SL; B. Paralectotype, ZMUC P92155, 25 mm SL (lack of distal pigmentation probably due to abrasion); C. ZMUC P921974, 26 mm SL; D. ZMUC P9251, 29 mm SL (a cotype of *M. niger*); E. LACM 33603-4, 30 mm SL; F. ZMUC P92210, 30.5 mm SL; G. LACM 33629-3, 35 mm SL; H. Lectotype, ZMUC P9260, 61 mm SL.

Melanocetus niger Regan 1925
Figures 21-24, 27, 30

Melanocetus niger Regan 1925:565 (original description, in part, 4 of 11 cotypes [see Comments, p. 79] all Gulf of Panama, lectotype hereby designated, ZMUC P9252, 80 mm, *Dana* stn. 1208(4), 6°48′N, 80°33′W, 3,500 m wire, 0810 h, 16 January 1922); Regan 1926:33, pl. 8, fig. 1 (in part, description, 4 additional females); Regan and Trewavas 1932:53, fig. 76B (in part, listed after Regan 1925, 1926); Beebe and Crane 1947:153-154 (in part, description of 4 additional females not seen by us); Bertelsen 1951:44, 53, table 4 (in part, description, comparison with all known material, in key); Grey 1956:237 (in part, synonymy, distribution).

Material. — Metamorphosed females, 6 (22-80 mm): BMNH 1925.8.11.29, 47 mm (paralectotype); IOAN uncatalogued, 77 mm; ZMUC P9254, 22 mm (paralectotype); ZMUC P9256, 37 mm (paralectotype); ZMUC P921973, 42 mm (*Galathea* stn. 727); ZMUC P9252, 80 mm (lectotype).

Males and larvae unknown.

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight; least outside width between frontals 14.3-24.3% SL; number of lower jaw teeth 37-57 (Figure 22); longest lower jaw tooth 6.9-10.5% SL (Figure 21); width of pectoral fin lobe 9.1-13.5% SL; escal bulb width 3.8-5.0% SL (Figure 23); illicium length 29.8-38.8% SL (Figure 24); esca without crests (Figure 27); integument relatively thick.

Description. — Escal bulb not compressed, with a low, rounded or conical distal prolongation nearly always pigmented on tip; anterior and posterior

crests absent (Figure 27); integument as in *M. johnsoni*.

Number of upper jaw teeth 29-86; dorsal fin rays 14-15; pectoral fin rays 18-21 (Table 2).

Distribution. — All six known specimens of *M. niger* were collected in the Gulf of Panama and adjacent waters of the eastern tropical Pacific Ocean as far west as approximately long. 90° W (see Distribution, p. 83). Eighty-three percent of the material was captured by open nets fished at maximum depths of 1,500 m and below.

Comments. — *Melanocetus niger* was briefly described by Regan (1925) from seven specimens collected in the Gulf of Panama without type designation and without a listing of individual sizes, station numbers, or other means of identification. Regan (1926) added four more specimens without providing means of separating the original seven. All 11 specimens bear labels indicating cotype status and all are treated here as part of the original type material. One of these is designated the lectotype (ZMUC P9252, 80 mm), three are referred to *M. polyactis* (BMNH 1925.8.11.30, 26 mm; ZMUC P9251, 29 mm; ZMUC P9253, 47 mm), three unidentifiable specimens are listed below as *Melanocetus* sp. (ZMUC P9255, 13.5 mm; BMNH 1925.8.11.31, 14 mm; BMNH 1925.8.11.28, 43 mm), and one is unaccounted for and presumed lost (*Dana* stn. 1209(3), 37 mm total length). The remaining three specimens are recognized as paralectotypes of *M. niger*.

Melanocetus eustalus n. sp.
Figures 18, 28, 30

Melanocetus ferox, Pietsch 1972b:10 (misidentification, luminescence); Brewer 1973:25 (after Pietsch 1972b, distribution).

Melanocetus sp. Pietsch 1976:782, 783 (reproduction).

Material. — A single female, the holotype, LACM 30037-12, 111 mm, *Velero IV* stn. 11748, eastern Pacific off Mazatlán, Sinaloa, Mexico, 21°39′ N, 106°58′ W, 3 m IKMT, 0-1,675 m, bottom depth 2,820 m, 1320-2136 h, 11 November 1967.

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight; least outside width between frontals 18.0% SL; number of lower jaw teeth 60; longest lower jaw tooth 5.9% SL; illicium length 30.6% SL; width of pectoral fin lobe 9.9% SL; escal bulb width 11.3% SL; esca without crests (Figures 18, 28); integument relatively thick.

Description of holotype. — Escal bulb large (length 14.4% SL), slightly compressed, with a low conical distal prolongation, pigment absent; pos-

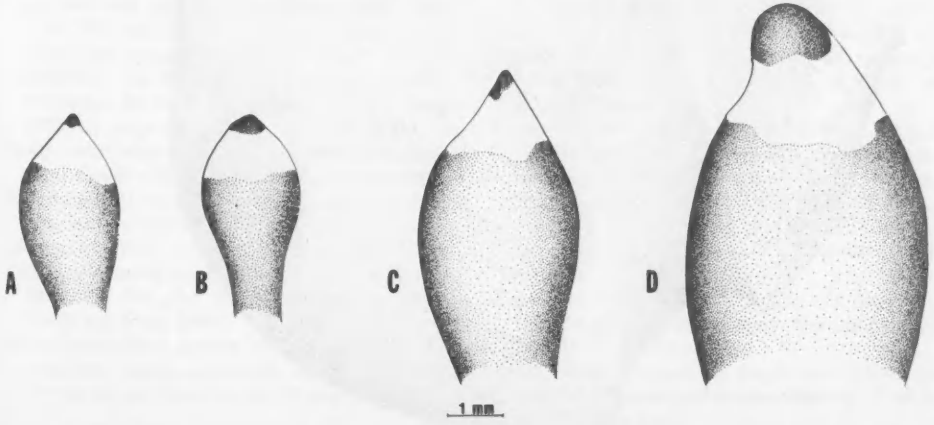

FIGURE 27.—Escae of *Melanocetus niger*: A. Paralectotype, ZMUC P9256, 37 mm SL; B. Paralectotype, BMNH 1925.8.11.29, 47 mm SL; IOAN uncatalogued, 77 mm SL; D. Lectotype, ZMUC P9252, 80 mm SL.

terior and anterior crests absent (Figure 28); integument as in *M. johnsoni*.

Gill opening exceptionally large, greatest diameter 23.4% SL; number of upper jaw teeth 91; vomerine teeth 8; dorsal fin rays 15; pectoral fin rays 16 (Table 2).

Etymology. — The name *eustalus* is derived from the Greek *eustales*, an adjective meaning well equipped, in reference to the enormous esca of this ceratioid.

Luminescence. — Upon capture, the holotype of *Melanocetus eustalus* was maintained alive for several minutes during which the bulb of the esca glowed continuously with a bright, golden-orange light. The amount of light actually emitted, however, appeared to be controlled by an up and down

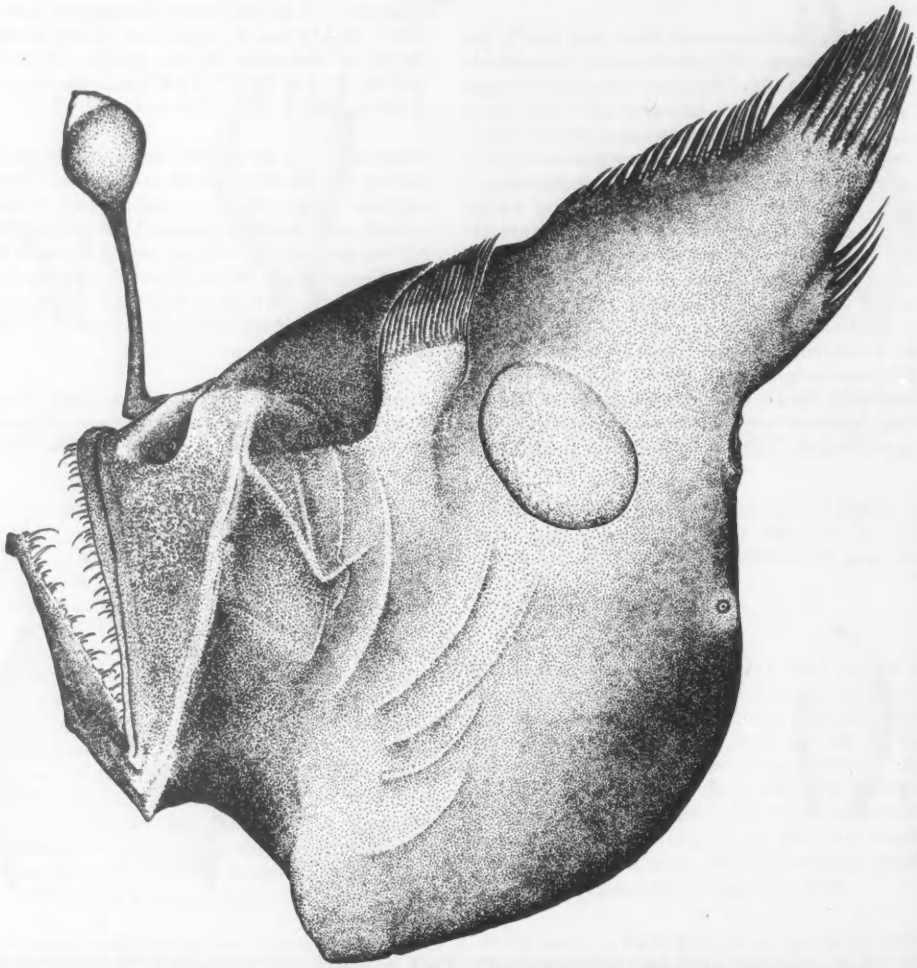

FIGURE 28.—Holotype of *Melanocetus eustalus*, LACM 30037-12, 111 mm SL, lateral view. Drawn by Elizabeth Anne Hoxie.

movement of the darkly pigmented, inner wall of the photophore of the esca. The glowing bulb was almost entirely covered and uncovered four or five times within a period of at least 1 min (B. G. Nafpaktitis[3]; see Pietsch 1972b). A mechanism of this kind would provide a rapid means of extinguishing light that may not only attract potential mates and prey, but also predators.

Melanocetus murrayi Günther 1887
Figures 2, 4, 5, 7-15, 16A, 19, 20, 29-31

Females

Melanocetus murrayi Günther 1887:57, pl. 11, fig. A (original description, two specimens, lectotype BMNH 1887.12.7.17, 71 mm, *Challenger* stn. 106, central Atlantic, 1°47′ N, 24°26′ W, 0-3,386 m); Regan 1926:32 (description, additional material, in key); Parr 1927:27 (description, additional material); Regan and Trewavas 1932:27, 49-50, fig. 22C, 23, 71 (description, additional material; pectoral radials, pelvic bone, escae figured; in key); Beebe 1932:99-102, fig. 29, 30 (description of postlarvae); Parr 1934:7 (listed); Fowler 1936:1143, 1144-1145, 1346, 1363, fig. 483 (after Günther 1887; Regan 1926; in key); Koefoed 1944:3, 5 (description, comparison, additional material); Fowler 1949:158 (listed); Bertelsen 1951:40-48, fig. 16, tables 4, 5 (description of females, males, larvae, comparison with all known material, in key); Grey 1955:299 (additional material, color); Grey 1956:234 (synonymy; distribution); Monod 1960:687, fig. 80 (pectoral radials); Pietsch 1972a:34, 38 (osteological comments); Maul 1973:667 (synonymy, after Bertelsen 1951).

Melanocetus bispinosus Günther 1880:473 (name only); Goode and Bean 1896:495 (in synonymy).

Melanocetus (Liocetus) murrayi Günther 1887:56 (original description, a distinct subgenus).

Liocetus murrayi, Goode and Bean 1896:495, fig. 407 (new combination, after Günther 1887); Gill 1909:583, 584, fig. 22 (after Günther 1887; Goode and Bean 1896).

Melanocetus vorax Brauer 1902:294 (original description, single specimen, holotype ZMHU 17710, 85 mm, *Valdivia* stn. 63, Gulf of Guinea, 2°00′ N, 8°04′ W, 0-2,492 m); Brauer 1906:320-321, pl. 15, fig. 4 (description after Brauer 1902). Fowler 1936:1143, 1144 (description after Brauer 1902, 1906; in key).

Melanocetus johnsoni, Brauer 1906:319 (misidentification); Regan 1926:33 (in part, misidentification); Murray and Hjort 1912:609, 614, 618, fig. 469 (misidentification); Fowler 1936, fig. 482 (figure after Brauer 1906).

Melanocetus krechi, Murray and Hjort 1912:614, 618 (in part, misidentification).

Melanocetus tumidus Parr 1927:28-29, fig. 10 (original description, single juvenile, holotype BOC 2022, 15 mm, *Pawnee* Third Oceanographic Expedition stn. 11, western North Atlantic, 23°58′ N, 77°26′ W, 2,135 m wire, 2 March 1927); Regan and Trewavas 1932:49 (mentioned); Grey 1956:239 (synonymy, distribution, a young female *M. murrayi*).

Melanocetus niger, Parr 1927:29 (misidentification); Beebe 1929:18 (misidentification).

Males

Rhynchoceratias acanthirostris Parr 1927:31, fig. 11 (original description, single specimen, holotype BOC 2011, 20 mm, *Pawnee* Third Oceanographic Expedition stn. 22, western North Atlantic, 23°37′ N, 77°15′ W, 2,135 m wire, 12 March 1927); Parr 1930b:130, 134 (anatomy, life history).

Rhynchoceratias latirhinus Parr 1927:32, 33, fig. 12 (original description, single specimen, holotype BOC 2012, 15 mm, *Pawnee* Third Oceanographic Expedition stn. 33, western North Atlantic, 24°11′ N, 75°37′ W, 2,440 m wire, 22 March 1927).

Rhynchoceratias longipinnis Parr 1930a:7, fig. 2-5 (original description, single specimen, holotype BOC 2592, 16 mm, *Pawnee* Third Oceanographic Expedition stn. 59, Bermuda, 32°19′ N, 64°32′ W, 2,440 m wire, 21 April 1927, osteology); Parr 1930b:129, fig. 1-3, 6, 7 (anatomy, life history).

Xenoceratias acanthirostris, Regan and Trewavas 1932:54, 55 (new combination; description after Parr 1927, in key).

Xenoceratias longipinnis, Regan and Trewavas 1932:54, 56 (new combination; description after Parr 1927, in key).

Xenoceratias latirhinus, Regan and Trewavas 1932:54, 57 (new combination; description after Parr 1927, in key).

[3]B. G. Nafpaktitis, Professor, Department of Biological Sciences, University of Southern California, Los Angeles, CA 90007, pers. commun. November 1967.

Xenoceratias regani Koefoed 1944:4, 6, pl. 1, fig. 6 (original description, single specimen, holotype UBNM 4311, 20 mm, *Michael Sars* North Atlantic Deep-Sea Expedition stn. 53, central North Atlantic, 34°59′ N, 33°01′ W, 2,600 m wire, bottom depth 2,615-2,865 m, 8-9 June 1910).

Melanocetus murrayi, Bertelsen 1951:44-48, fig. 16A, D, F, H, table 5 (synonymy, description, comparison with all known material, in key); Grey 1956:235 (synonymy, distribution); Maul 1962b:37-38, fig. 3 (description of additional specimen); Maul 1973:667 (synonymy, after Bertelsen 1951).

Material.—Metamorphosed females, 140 (13.5-120 mm): BMNH, 8 (21-57 mm); BOC, 1 (15 mm); CAS, 3 (14.5-51 mm); FSM, 6 (13.5-54 mm); IOAN, 5 (14-56 mm); IOS, 6 (17-68 mm); ISH, 33 (15-120 mm); LACM, 14 (13-84 mm); MCZ, 14 (13-84 mm); UMML, 28 (17-99 mm); USNM, 7 (15-78 mm); VIMS, 1 (33 mm); ZMUC, 14 (14-80 mm).

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer deeply concave (Figure 2); least outside width between frontals 9.1-17.8% SL (Figure 19); number of lower jaw teeth 46-142 (Figure 20); longest lower jaw tooth 7.7-16.7% SL; width of pectoral fin lobe 6.1-8.9% SL; escal bulb width 1.9-5.1% SL; illicium length 23.1-37.2% SL; esca with crests minute or absent (Figure 29); minute skin spines restricted to caudal peduncle; integument relatively thin (0.48 mm).

Description. — Escal bulb not compressed, with a low, rounded distal prolongation usually unpigmented on tip; posterior and anterior crests minute or absent (Figure 29); integument thin, easily torn (cross sections measure 0.48 mm in thickness), pigment readily lost during fixation and preservation, often transparent, especially in gill region and over branchiostegal rays.

Number of upper jaw teeth 34-178; dorsal fin rays 12-14, pectoral fin rays 15-19 (rarely 20) (Table 2).

Distribution. — *Melanocetus murrayi* has a wide horizontal distribution in the Atlantic and Pacific, but is apparently absent from the Indian Ocean (see Distribution, p. 83). Compared with *M. johnsoni*, it is a much deeper living form: only 10% of the material (for which data was available) was captured in open nets fished at maximum depths of <1,000 m. Approximately 58% of the material was taken by gear fished at maximum depths of 1,500 m or below, and 45% by gear fished at 2,000 m or below (see Distribution, p. 83). The relatively thin integument of *M. murrayi* (less than one-third the thickness of that of its congeners) as well as a lighter, less well-ossified skeleton reflects the poorer trophic economies of these greater depths (see Description above).

FIGURE 29.—Escae of *Melanocetus murrayi*: A. ISH 2961/71, 58 mm SL; B. ISH 922/68, 70 mm SL; C. ISH 2961/71, 76 mm SL; D. ISH 375/73, 120 mm SL.

Comments. — *Melanocetus vorax* Brauer (1902) was tentatively synonymized with *M. murrayi* by Regan (1926). This decision was confirmed by Regan and Trewavas (1932) and later by Bertelsen (1951). *Melanocetus tumidus* Parr 1927 (not mentioned by Bertelsen 1951) was based on a single metamorphosing female (15 mm) that fits well within the larval and metamorphosing material of *M. murrayi* (Bertelsen 1951) in lacking pigment on the caudal peduncle and having a faintly pigmented gill cover. This nominal form is hereby synonymized with *M. murrayi*.

Species Incertae Sedis

The following two nominal species based on males are distinguished from other *Melanocetus* males in having the posterior nostril well separated from the eye. They are probably not specifically distinct from each other and are most likely the males of one of the above recognized species based on females (Bertelsen 1951, fig. 20).

Melanocetus longirostris (Regan and Trewavas 1932) Incertae Sedis

Xenoceratias longirostris Regan and Trewavas 1932:54, 55, fig. 80 (original description, single specimen, holotype ZMUC P9259, 21 mm, *Dana* stn. 3751(7), north of New Guinea, 3°40′ N, 137°53′ E, 3,000 m wire, 1240 h, 12 July 1929); Fowler 1936:1346 (after Regan and Trewavas 1932; type species designation).

Melanocetus longirostris, Bertelsen 1951:42-44, 54 (new combination, comparison with all known material, in key); Grey 1956:238 (synonymy, distribution after Bertelsen 1951).

Melanocetus nudus (Beebe and Crane 1947) Incertae Sedis

Xenoceratias nudus Beebe and Crane 1947:155, text fig. 2 (original description, single specimen, holotype CAS-SU 46495 [originally NYZS 28402], 21.5 mm, Eastern Pacific *Zaca* Expedition stn. 210T-8, south of Cape Blanco, Costa Rica, 9°12′ N, 85°10′ W, 915 m, 27 February 1938).

Melanocetus nudus Bertelsen 1951:43-44, 54, fig. 20 (new combination, description of one additional specimen, comparison with all known material, in key); Grey 1956:238 (synonymy, distribution after Bertelsen 1951).

Melanocetus species

The following females, all considered to be part of the original type material of *M. niger* (see Comments, p. 79), are so poorly preserved that they cannot be referred to any described species of the genus: BMNH 1925.8.11.31, 14 mm; ZMUC P9255, 13.5 mm; BMNH 1925.8.11.28, 43 mm (illicium absent).

The following males cannot be satisfactorily identified to species based on females. Variation in the number of denticular teeth and pectoral fin rays and in the subdermal pigmentation (Bertelsen 1951) is considerably greater than previously thought (see Diagnosis of family above): LACM, 73 (11.5-24 mm) (66 from Hawaii at lat. 21°20-30′ N, long. 158° 20-30′ W; 3 from the Banda Sea; 2 from the Mid-American Trench at approximately lat. 18° N, long. 104° W; and 2 from the Equator at about long. 170° E and 145° W).

DISTRIBUTION

The family Melanocetidae is widely distributed throughout all three major oceans of the world in a broad belt limited by the Arctic and Antarctic Polar Fronts, with northern and southernmost records at approximately lat. 62° N and 46° S. It is present in the Gulf of Mexico, but has not been collected in the Gulf of California or the Mediterranean Sea (Figure 30).

Two of the five species of the family are wide ranging forms: *M. johnsoni* occurs throughout the Atlantic, Pacific, and Indian Oceans; *M. murrayi* is found throughout the Atlantic and Pacific Oceans but has so far not been recorded from the Indian Ocean. Two lesser known species, *M. polyactis* and *M. niger*, are restricted to the eastern tropical Pacific Ocean. *Melanocetus eustalus* is represented by a single specimen collected in the eastern Pacific off Mazatlán, Sinaloa, Mexico.

Since the majority of collections of melanocetids were made with nonclosing nets, the actual depth of capture is unknown. Furthermore, because sample sizes are small a statistical treatment of the nonclosing net data is impossible. Assuming, however, that most specimens were caught at depths where gear is fished for the longest period of time, vertical distributions may be roughly estimated by referring to the maximum depth reached by gear for each capture. On this assumption, members of the Melanocetidae may be taken anywhere between 250 m and some unknown

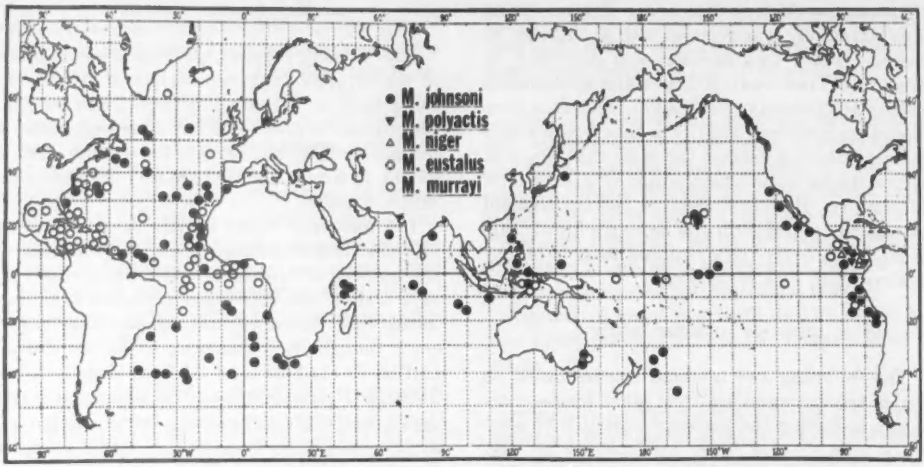

FIGURE 30.—Geographical distribution of *Melanocetus* species. Symbols may indicate more than one capture.

lower depth limit exceeding 3,000 m, but they are commonly found between roughly 500 and 2,500 m. *Melanocetus johnsoni* is most often collected between 500 and 1,500 m. *Melanocetus murrayi* is a considerably deeper dwelling species; the bulk of the known material was collected between 1,000 and 2,500 m (Figure 31). The relatively thin integument (see Description above) and lighter, less well-ossified skeleton of *M. murrayi* reflects the poorer trophic economies of these greater depths. The remaining species of the genus are so poorly represented in collections that their vertical distributions cannot be estimated.

EVOLUTIONARY RELATIONSHIPS

The Melanocetidae appears to be a relatively underived ceratioid family (Bertelsen 1951; Pietsch 1972a, 1976, 1979). The five species are characterized by a confusing mosaic of primitive and derived character states such that an interpretation of interspecific phylogenetic relationships is difficult. In any case, however, it seems apparent that *M. murrayi* has split off from the main line of melanocetid evolution and acquired a number of unique features that reflect its most derived position in the genus: 1) depressed cranium, 2) concave vomer, 3) small pectoral fin, 4) tiny escal bulb, and 5) thin integument. Living in considerably deeper strata than its congeners most probably also reflects a derived condition.

The four remaining species are much more closely related to each other than any is to *M. murrayi*. Five characters can be used to distinguish these forms: 1) number of lower jaw teeth, 2) longest lower jaw tooth, 3) illicium length, 4) escal bulb width, and 5) escal morphology. Unfortunately, all but the last of these characters overlap in variation among the remaining forms of the genus, and, furthermore, the relative primitiveness of character states among these features is nearly impossible to determine. *Melanocetus johnsoni* is perhaps derived in having a relatively long illicium, and in having fewer, but longer jaw teeth (see Pietsch 1972b, 1974, 1975). *Melanocetus polyactis* and *M. niger* are similar in having relatively short jaw teeth, a similar escal morphology lacking anterior and posterior crests, and a sympatric geographic distribution that is restricted to the Gulf of Panama and adjacent eastern tropical Pacific. *Melanocetus eustalus* is derived in having an extremely large escal bulb, comparable with no other known ceratioid.

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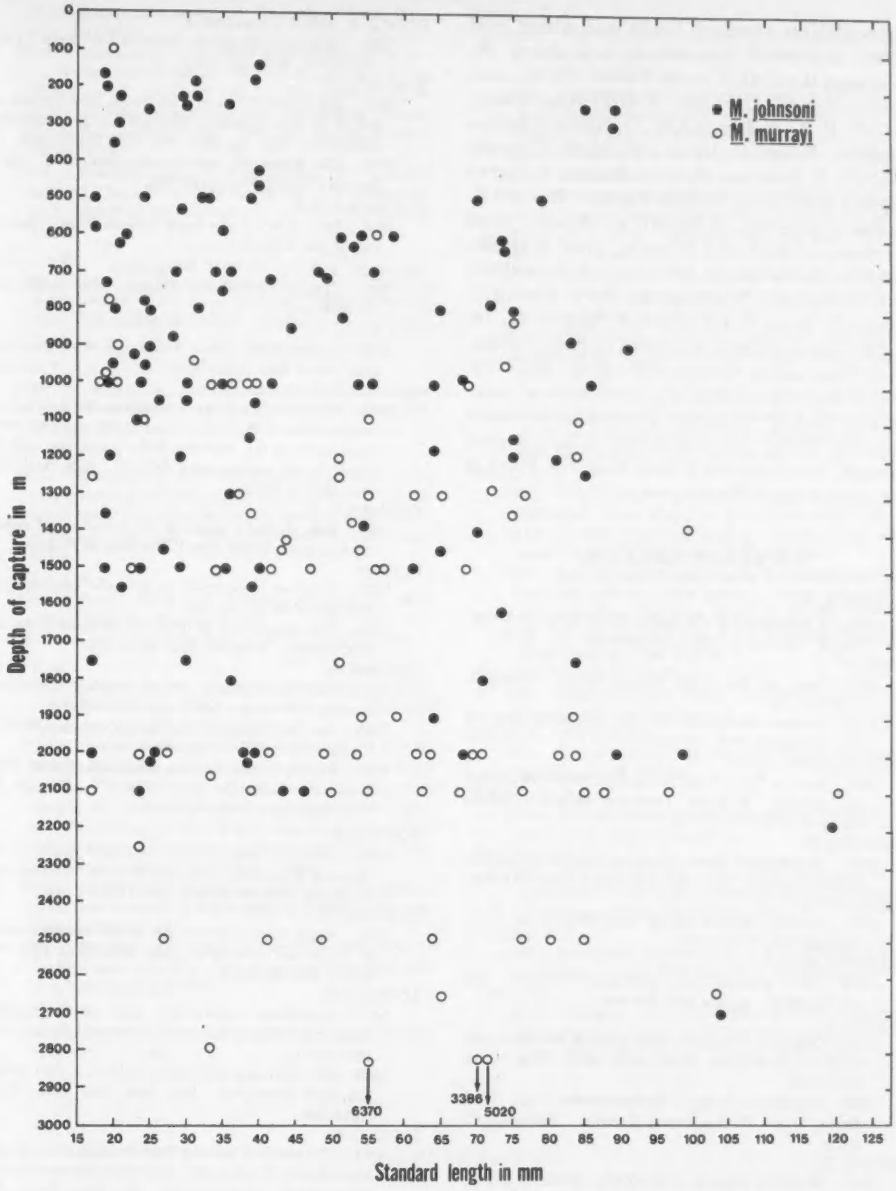

FIGURE 31.—Relationship between depth of capture (based on maximum depth reached by fishing gear) and standard length for two species of *Melanocetus*.

Merrett (IOS), Gerhard Krefft and Alfred Post (ISH), Robert J. Lavenberg and Jerry W. Neumann (LACM), Karsten Hartel (MCZ), Jack Moreland and C. D. Paulin (NMNZ), Allen Emery (ROM), P. A. Hulley (SAM), C. Richard Robins (UMML), Robert H. Gibbs and Susan Karnella (USNM), E. Bertelsen (ZMUC), Thomas A. Clarke (Hawaii Institute of Marine Biology), Richard E. Young (University of Hawaii at Manoa), Brett Stephenson (Auckland Museum, New Zealand), and Don A. Robertson (Ministry of Agriculture and Fisheries, Wellington, New Zealand). Elizabeth Anne Hoxie provided Figures 17, 18, and 28. The work was supported by National Science Foundation Grants GB-40700, DEB 76-82279 and DEB 7826540, the National Geographic Society, and PHS Biomedical Research Support Grant No. RR-07096 administered through the Graduate School Research Fund of the University of Washington.

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EARLY LIFE HISTORY OF PACIFIC MACKEREL, *SCOMBER JAPONICUS*

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ABSTRACT

The early life history of Pacific mackerel, *Scomber japonicus*, is described from laboratory-rearing studies and examination of stomach contents of sea-caught larvae. At 19° C mackerel eggs hatched in 56 hours, larvae were 3.1 mm standard length with a dry weight of 0.04 mg of which 50% was yolk. First feeding occurred 46 hours after hatching; all larvae fed by 60 hours (age 2.5 days). Larvae were then 3.6 mm long with fully pigmented eyes and 10% of the yolk remaining. Starvation was irreversible if larvae were not fed before age 4.5 days. Metamorphosis (15 mm standard length) occurred in 24 days at 16.8° C to 16 days at 22.1° C. Larvae 3-5 days old consumed 57% of their body weight per day and had a mean gross growth efficiency in dry weight of 33%. Oxygen consumption was 6.1 μl O_2 per milligram dry weight per hour at 18° C and 11.4 μl O_2 per milligram dry weight per hour at 22° C. Swimming speeds ranged from 1.3 standard lengths per second for first-feeding larvae to 3.8 standard lengths per second for fish at metamorphosis. Fifty percent of the larvae were able to capture a prey when the width of the prey was 85% of the width of the mouth and 95% were able to do so when the prey was 57% of the width of the mouth. Cannibalism was common in rearing groups; at 8 mm standard length, 50% of the larvae became capable of feeding on other fish larvae and cannibalism ceased when schooling commenced. Chief food items of sea-caught larvae were stages of copepods; maximum food width increased rapidly with larval length and was equivalent to the maximum mouth width. Mean prey width was 38% of mouth width. The larger organisms, constituting half of the prey eaten, accounted for 85-90% of the total volume of food eaten.

The development and distribution of eggs and larvae of the western Pacific population of the Pacific mackerel, *Scomber japonicus*, has been described (Kramer 1960; Kramer and Smith 1970), but little information exists on growth, behavior, and physiology of the larval stages. Incubation times and other data are known for the Japanese population of *S. japonicus* (Watanabe 1970). This paper provides some of the information needed to characterize the early life history of Pacific mackerel, including incubation times, yolk absorption, onset of feeding, vulnerability to starvation, swimming and feeding behavior, food ration, and oxygen consumption.

METHODS

Laboratory Experiments and Sea Samples

Eggs were obtained from Pacific mackerel maintained in spawning condition in the laboratory and induced to spawn by hormone injection (Leong 1977). Effects of temperature on incubation time were determined by placing test tubes containing 10 eggs and 25 ml of seawater in a temperature block set to produce a temperature gradient of 11.1°-23.3°±0.2° C (2 SE (standard error)) (Lasker 1964). Hatched eggs were counted at 2-4 h intervals and time from fertilization to 50% hatch estimated. Rate of yolk absorption was determined at 19.4°±0.4° C by measuring the surface areas of the yolk-sac and oil droplet from tracings made with an optical comparator (Wolfson 1965). Six samples, each of 15-25, larvae were taken over the first 72 h after hatching.

To estimate the time of first feeding at 18.9°±0.3° C, groups of larvae without past feeding experience were transferred to a 100 l container containing 150 rotifers/ml (*Brachionus plicatilus*). Four hours later, they were removed and the percentage of larvae that fed and the mean number of rotifers in the gut were calculated. Eight groups of 10-39 larvae were tested at periods from 18 to 114 h after hatching.

A starvation-based mortality curve was established at 19.0°±0.3° C by starting with 1,000 eggs in each of two 200 l containers, and counting and removing dead larvae daily. The age was determined at which starvation became irreversible in first-feeding larvae. Seven hundred and fifty eggs were incubated in each of four 200 l tanks and the resulting larvae were fed for the first time at

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ages 2.5, 3.5, 4.5, and 5.5 d. The percentage survival was determined on the eighth day. Larvae were fed rotifers (50/ml) on the first day of feeding, and rotifers and copepods (*Tisbe* sp.) thereafter.

Vulnerability of newly metamorphosed Pacific mackerel (mean length 16.7 mm SL (standard length)) to starvation was tested at 18.9°±0.2° C by transferring fish from the rearing container to containers without food. One group of fish was starved for 4 d, another for 5 d, and a third was fed *Artemia salina* nauplii. The two starved groups were fed at the end of the starvation period.

Tail beat frequency and amplitude of larval Pacific mackerel (3-5 mm SL) were determined for routine swimming and burst speeds by analysis of cine films taken at 100 frames/s using techniques described by Hunter (1972). Routine swimming speeds of larval mackerel, at 19° C, were measured by counting the number of squares crossed by a larva (3.7-6.6 mm SL) as it swam over a 1 cm grid on the bottom of the rearing tank for 9-153 s; a 3 cm grid was used for larger larvae (7.9-13.1 mm SL) with shorter observation times (3-46 s). The mean of 15-25 visual observations was used as an estimate of speed for the mean length of the larvae in the tank on the day of observation; speeds were adjusted for parallax caused by the difference in depth between the grid and the fish. Speeds of juveniles (>19 mm SL) were measured by timing the fish as they swam a measured distance (35-201 cm) around the perimeter of the rearing tank; in this case mean speeds were for individual fish and observation times ranged from 3 to 26 s.

The size at which Pacific mackerel larvae were capable of ingesting various prey was evaluated by placing them in a 110 l container with the prey and estimating the number that fed by examination of stomach contents. The type of prey, mean prey size, prey density, and duration of feeding respectively were: yolk-sac anchovy larvae, 2.7 mm SL, 8/l, 2 h; *A. salina* nauplii, 0.2 mm wide, 11/l, 4 h; and anchovy eggs, 0.67 mm wide, 10/l, 2 h. The mouth width, prey width, and standard length of the larvae were measured and percentage feeding success was estimated for size classes of larval length and mouth width. The number of fish per size class was >9. Size thresholds for 50% feeding success and 95% success were estimated by probit analysis (Finney 1952) and expressed as a function of mean larval length, or mean prey width/mean mouth width.

The sizes of food items eaten by Pacific mackerel larvae in the sea was determined by examination of the stomachs of 86 larvae taken in routine ichthyoplankton surveys along the California coast. We recorded the length of each larva and the number and maximum width of all identifiable food items (Arthur 1976; Shirota 1970).

Food requirements were estimated by feeding the rotifer *Brachionus plicatilis* to 3-5 d old Pacific mackerel larvae. Seven to eight samples of 9-16 larvae each were taken over each of three 12-h feeding days, the number of rotifers in the guts of each larva were counted, and the counts converted to equivalent dry weight using the conversion factor of 0.16 μg/rotifer (Theilacker and McMaster 1971). Daily changes in larval weight were estimated from mean standard lengths using a length-dry weight conversion given in the results. The rate of gastric evacuation for 4 mm SL larvae was measured. They were allowed to feed for 4 h and then transferred to a tank without food; samples of 13-16 larvae were taken at about hourly intervals until the stomachs were empty. The number of rotifers in stomachs were counted and converted to dry weight, and the rate of gastric evacuation was estimated in terms of dry weight. The daily ration was estimated from the mean stomach contents and the rate of gastric evacuation. Gross growth efficiency was estimated in terms of dry weight from the daily ration and weight gain over 24 h.

Metabolic requirements of Pacific mackerel larvae were estimated using a Warburg respirometer and standard manometric techniques (Umbreit et al. 1964) to measure oxygen consumption. One or more Pacific mackerel larvae were added to an 18 ml Warburg flask filled with 4.4-8.7 ml of filtered seawater (salinity 33.58-33.93‰). Larvae >0.06 mg dry weight were tested individually. Twenty-one tests were made at 18.0°C of larvae or groups of larvae ranging in length from 3.7 to 17.9 mm SL (0.038-12.74 mg) and 14 at 22.0° C, of larvae 3.2-10.5 mm SL (0.025-2.86 mg). Flasks were shaken at 102 times/min for 5 out of every 30 min; readings were taken after the first 2 h and continued for 150-360 min. At the end of a test, larvae in each flask were measured, rinsed in distilled water, oven dried to a constant weight, and weighed. Mean weight was obtained for fish tested in groups. All runs were made under normal room illumination, about 700 lx. Log_{10} oxygen consumption in microliters O_2 per hour was regressed on $\log_{10}$ body weight for the 18.0° and 22.0° C experiments. As the slopes were close to unity, oxygen consumption was expressed in microli-

ters per milligram per hour. Metabolic requirements were compared with daily ration by converting oxygen consumption and daily ration to calories (1 μl O_2 = 0.005 cal: one *Brachionus plicatilis* = 0.00085 cal, Theilacker and McMaster 1971).

Culture of Larvae

Seven groups of Pacific mackerel were reared to metamorphosis to determine growth rates and effects of temperature on growth. The rearing containers were black fiber glass, cylindrical tanks (122 cm in diameter × 36 cm deep). Culture volume increased during the rearing period from 200 to 400 l because of the addition of seawater containing food and algae. Tank temperature was controlled by a regulated water bath, and groups were reared at temperatures ranging from 16.8° to 22.1° C. Illumination at the water surface during the 12-h day was about 2,000 lx. Tanks were started with 3,000 eggs/group. Initially, larvae were fed laboratory-cultured *Brachionus plicatilis*. At age 5 d, laboratory-cultured copepodids and adult copepods (*Tisbe* sp.) were added; 200,000 copepods were added daily until metamorphosis. Initially 30 or more rotifers/ml were added for the first few days of feeding; thereafter the density of rotifers was allowed to decline. On a diet of rotifers alone, growth slowed after larvae reached 5 mm SL and few larvae survived longer than 15 d. Newly metamorphosed juveniles were fed live and frozen adult *A. salina* and minced squid (*Loligo opalescens*) and northern anchovy. From 1 to 6 l of algal culture, *Tetraselmis* sp. (300,000-500,000 cells/ml), were added daily to provide food for rotifers and copepods. Samples of 10 or more larvae were taken on alternate days for length measurements. Some samples were washed in distilled water, dried, and subsequently weighed to obtain a relation between length and dry weight.

RESULTS

Hatching, Onset of Feeding and Starvation

Eggs of Pacific mackerel are transparent spheres, ranging in diameter from 1.06 to 1.14 mm (Kramer 1960). Incubation times ranged from 33 h at 23° C to 117 h at 14° C (Figure 1); eggs did not hatch below 14° C. The curve for hatching time as a function of temperature for the western Pacific population (data from Watanabe 1970) appears to be the same as the one for the eastern Pacific population.

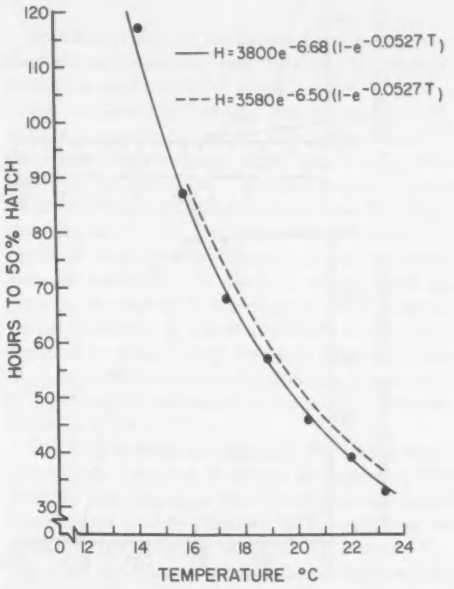

FIGURE 1.—Incubation time (fertilization to 50% hatch) of *Scomber japonicus* eggs. Solid line is for present data, points are estimated time to 50% hatch of eggs in five test tubes per temperature, dashed line is for data of Watanabe (1970). The general equation was developed by Zweifel and Lasker (1976) and fit to the 50% values.

At hatching, larvae averaged 3.1 mm SL (Figure 2B) and weighed 0.040 mg dry weight, of which 50% was yolk. At 19° C, first feeding occurred 46 h after hatching; by 60 h after hatching, all larvae had ingested one or more rotifers in 4 h (Figure 2D). Thus the 50% threshold for onset of feeding at 19° C occurred at about 50 h (2 d) after hatching. At this time larvae were 3.6 mm SL, the eyes were fully pigmented and 10% of the yolk remained, principally the remnants of the oil droplet (Figure 2A, B). Over the threshold for the onset of feeding, the mean number of rotifers in Pacific mackerel stomachs increased from 2 at 46 h to 14 at 68 h (Figure 2E). The larvae in each group had no previous feeding exposure, hence the increase in feeding activity with time could not be attributed to experience.

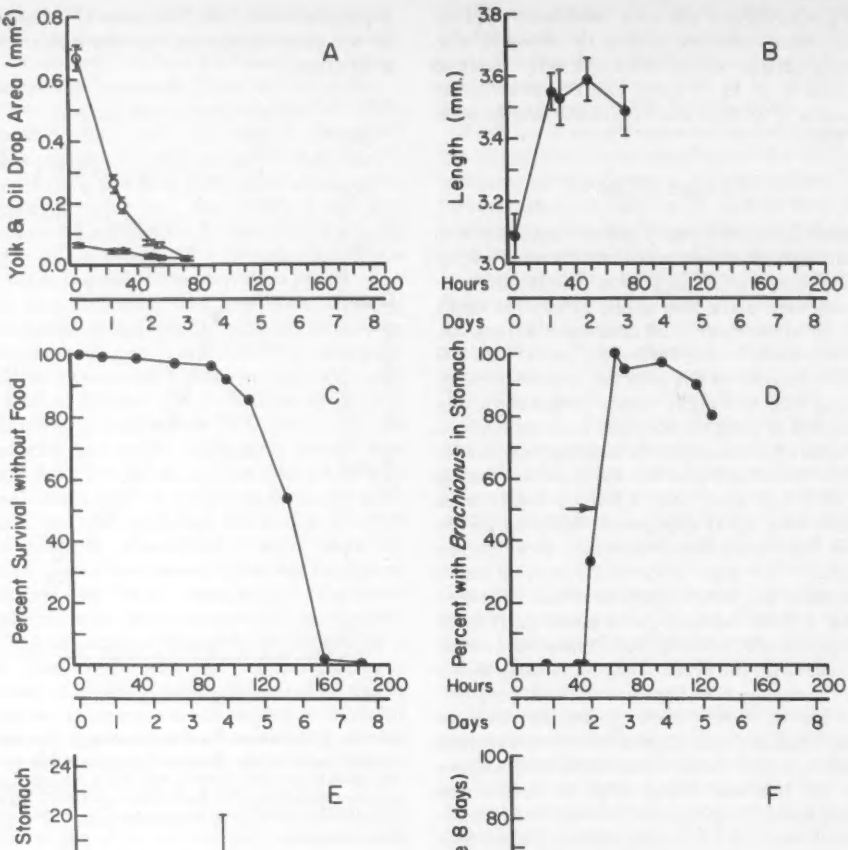

FIGURE 2.—Yolk absorption, onset of feeding, starvation, and point of irreversible starvation in Pacific mackerel larvae at 19° C: A. Rate of yolk absorption—open circles mean area of yolk-sac, solid circles mean area of oil droplet (mm²). B. Mean length of larvae from hatching through yolk-absorption. C. Percent survival of larvae without food. D. Percent of larvae tested at various times after hatching that had ingested one or more *Brachionus plicatilis* in a 4-h test period—arrow indicates the 50% threshold for the onset of first feeding. E. Mean number of *B. plicatilis* per positive stomach of larvae tested at various times after hatching. F. Percentage survival at age 8 d for larvae fed for the first time at age 2.5, 3.5, 4.5, and 5.5 d—percentages are plotted at the time food was first added. Bars in A, B, and E represent ±2 SE of mean.

If larvae were not fed, most died between ages 4 and 7 d and none survived longer than 7 d (Figure 2C). Highest survival (on the eighth day after hatching) occurred when food was added for the first time at age 2.5 d; survival was somewhat lower if food was added at 3.5 d and negligible if added at 4.5 d (Figure 2F). Thus at 19° C starvation appeared irreversible if food was not provided before 4.5 d.

Pacific mackerel larvae, unlike herring or anchovy (Blaxter and Hempel 1963; Lasker et al. 1970), did not cease swimming or feeding at the time of irreversible starvation. At age 5 d, the incidence of larvae with rotifers in their stomachs was relatively high (80%) (Figure 2D), but the average number of rotifers per positive stomach was much less than in larvae fed first at age 2 or 3 d (Figure 2E). Thus at age 5 d, most larvae were still able to feed, but owing to their weakened condition, none were able to capture enough prey to survive.

Vulnerability of larvae to starvation persisted through metamorphosis. All juvenile Pacific mackerel appeared emaciated and swam slowly by the fourth day of starvation. Mortality of 10% occurred in the group starved 4 d; 50% mortality occurred in those fish starved 5 d. All juveniles surviving 4 and 5 d of starvation recovered when food was added; no mortality occurred in the controls. Thus, newly metamorphosed Pacific mackerel were able to withstand 1 or 2 d more of starvation than first-feeding larvae, but they were better able to recover from food deprivation.

Growth

Growth in length of Pacific mackerel larvae was slow and almost linear over the first 10-15 d until larvae reached about 6-7 mm SL; there followed a rapid acceleration through metamorphosis. We did not fit equations to these data because none of the standard growth equations gave a good fit to the entire growth curve. The effect of temperature on growth was not distinguishable over the initial growth period, but became obvious during the period of rapid growth (Figure 3, Table 1). To provide an index of the effect of temperature on growth, we expressed the duration of the larvae period (hatching to metamorphosis, 15 mm) as a function of temperature (inset in Figure 3). The Q_{10} was 3.0 when calculated from the equation in Figure 3 for the temperature range of our observations (16.8°-22.1° C).

The length-weight relation for Pacific mackerel larvae and juveniles is shown in Figure 4. The form of this equation was developed by James Zweifel and used by Hunter (1976) to express the length-weight relation for northern anchovy larvae. The curvilinear nature of the length-weight relation, still evident in the log-log plot (Figure 4), indicates that if a linear regression of $\log_{10}$ weight

TABLE 1.—Growth data (millimeters SL) for seven groups of *Scomber japonicus* larvae reared at different mean temperatures from hatching through metamorphosis.

Age (days)	22.1° C[1]			20.4° C			19.6° C			19.5° C			19.2° C			18.9° C			16.8° C		
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD
1										10	3.1	0.24							31	3.5	0.12
2	14	3.3	0.21	16	3.8	0.06	16	3.7	0.10	15	3.9	0.09	15	3.8	0.06						
3	14	3.5	0.30																		
4	10	3.6	0.22	18	3.8	0.26	33	4.2	0.23	10	4.0	0.17	15	4.0	0.20	10	3.7	0.20			
5																					
6	10	3.9	0.21	15	4.2	0.41	15	4.8	0.44	13	4.2	0.14	15	4.4	0.37	10	4.1	0.39	15	4.3	0.42
7										27	4.5	0.40									
8	12	4.5	0.55	15	5.7	0.77	15	6.0	0.39	25	4.7	0.56	15	5.0	0.40				15	5.1	0.43
9													5	5.9	0.13						
10	12	6.0	1.13	15	6.3	0.91	15	6.6	0.70	15	4.8	0.43	19	5.6	0.77	11	5.2	0.45			
11																			15	6.5	0.70
12	22	8.4	1.88	16	8.2	1.31	15	6.5	0.75	11	5.9	1.08	25	6.4	0.68	12	6.1	0.60	15	7.0	0.50
13																					
14	10	8.9	1.46	10	11.5	1.54	15	8.4	1.12	30	6.4	1.09	15	6.6	0.80				17	7.7	1.40
15																			11	8.1	1.08
16	10	14.9	1.45	15	14.1	2.01	15	8.9	1.76	16	8.5	2.21	15	7.1	0.81	13	7.6	1.50			
17										10	10.0	2.71				12	9.0	1.33	15	10.3	2.11
18				15	17.8	1.70	15	10.3	2.48				15	10.3	3.21	13	9.4	1.61	17	10.8	2.84
19	15	24.1	5.81																		
20							15	12.5	3.18	17	17.7	4.21	15	11.7	2.88				9	11.5	2.81
22							15	17.5	4.51				15	14.6	4.62						
23																15	13.7	1.26			
24							24	20.4	5.10				16	18.5	5.38	10	19.8	2.36			
25																			17	17.1	5.07

[1]Juvenile growth (age, *n*, $\bar{x}$, and (SD)): 26 d, 13, 34.4 mm (4.37); 29 d, 9, 43.9 mm (3.60); 39 d, 5, 55.0 mm (8.74); and 47 d, 9, 67.3 mm (10.30).

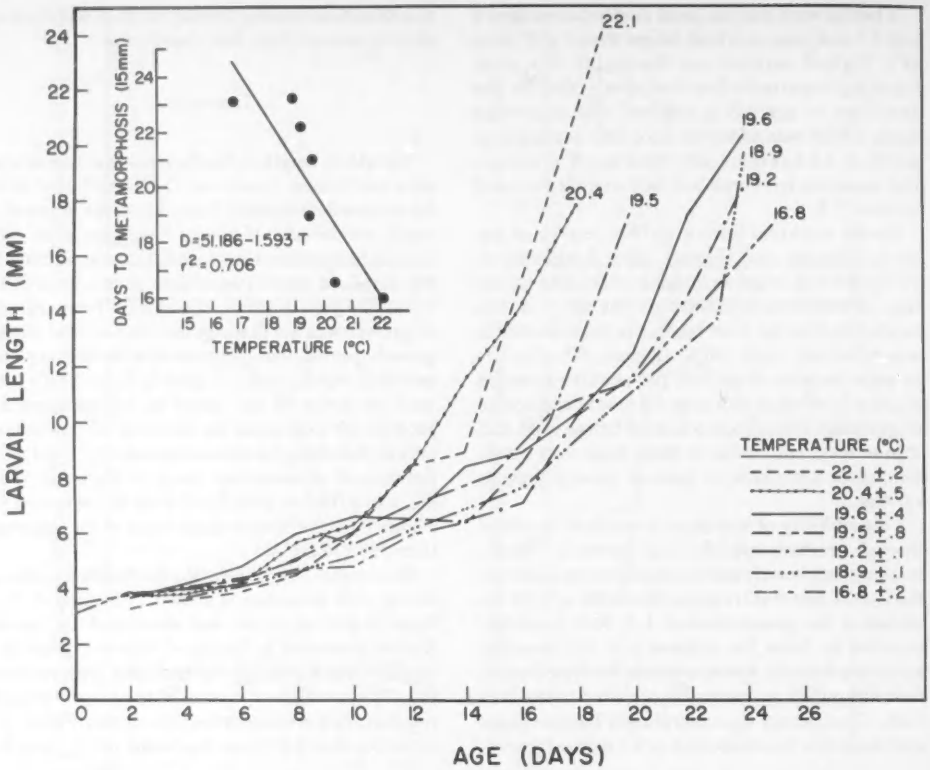

FIGURE 3.—Growth of seven groups of Pacific mackerel larvae reared in the laboratory from hatching (age 0 d) through metamorphosis (15 mm SL). Lines connect means given in Table 1; rearing temperatures (±2 SE) given on right side of figure and at end of lines. Inset at top: elapsed time (days) from hatching to metamorphosis (15 mm), as a function of rearing temperature.

on $\log_{10}$ length were used, it would produce inaccurate estimates.

Swimming Behavior

At typical cruising speeds, larval Pacific mackerel (3-5 mm SL) have a high tail beat frequency of about 30 beats/s and a low tail beat amplitude of 0.16 standard length. At slow speeds, tail beat frequency remained relatively constant but the amplitude of the tail beat changed. At higher speeds, both amplitude and frequency changed but the relative increase in amplitude was much greater than that of frequency (Table 2). Thus larval Pacific mackerel, unlike the adults (Hunter and Zweifel 1971), predominantly modulate tail beat amplitude to effect changes in speed.

Cruising speeds of Pacific mackerel increased markedly over the larval period from 0.46 cm/s (1.3 standard body lengths/s) for first-feeding larvae (3.6 mm SL) to 5.6 cm/s (3.8 standard body lengths/s) for fish at metamorphosis (Figure 5). This differs from the pattern in adult fishes where speed relative to size decreases with an increase in fish size (Webb 1975).

Feeding Behavior

Upon sighting a prey (rotifer or copepod), a Pacific mackerel larva advanced toward the prey,

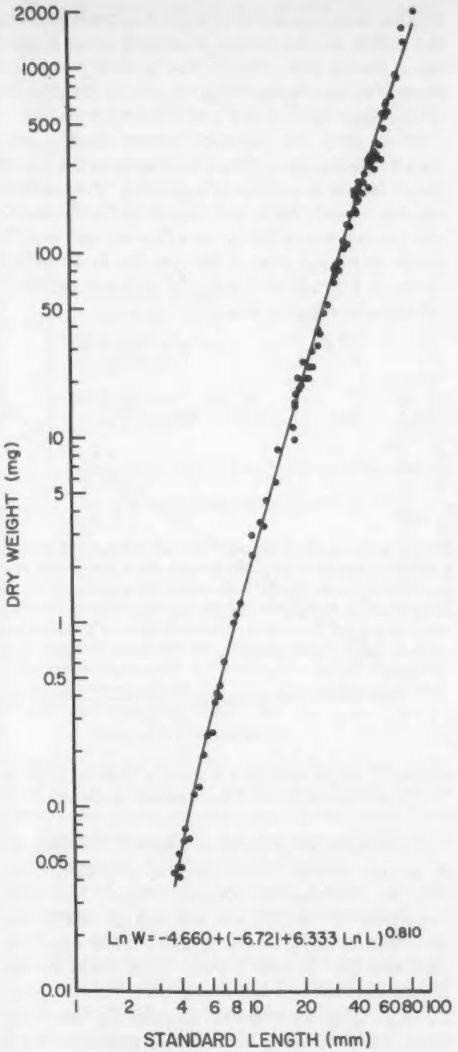

FIGURE 4.—Relation between dry weight (W) of larval and juvenile Pacific mackerel in milligrams and standard length (L) in millimeters. Points are observed values for individuals >18 mm and for larvae <18 mm; points are means for groups of 15 larvae.

stopped, drew back the tail, and held it in a slightly recurved, high amplitude position while the rest of the body remained relatively straight.

TABLE 2.—Tail beat frequency and amplitude and speed of 3-5 mm larval Pacific mackerel ($\bar{x}$ = 4.23 ± 0.09 mm SL) expressed as a function of standard length.

N	Swimming speed (SL/s) Class interval	Mean	Tail beat Frequency (beats/s)	Tail beat Amplitude/SL
18	0.01- 1.0	0.58	33.2	0.12
30	1.01- 2.0	1.48	30.2	0.16
9	2.01- 3.0	2.48	30.2	0.17
3	3.1 - 5.0	4.00	37.5	0.18
3	10.1 -15.0	12.18	39.4	0.29
1	—	37.04	38.9	0.33

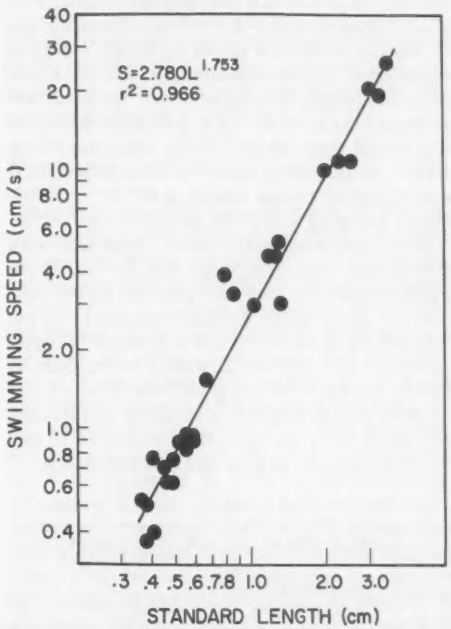

FIGURE 5.—Relation between swimming speed and standard length of Pacific mackerel larvae ($\log_{10}$ scales) at 19° C. Each point <2.0 cm is the mean of 15-25 observations. For ≥2.0 cm, individual fish were measured.

Feeding involved driving the tail posteriorly and opening the mouth. Larvae often attacked the same prey two or more times if the previous strike was unsuccessful, and repositioned for subsequent strikes by moving backward. Handling times were negligible because the prey was engulfed instantaneously. Older Pacific mackerel larvae developed a set of motor patterns for feeding on fish larvae; larvae were seized from the side and carried crosswise in the mouth. Larger prey were repeatedly released and grasped until they ceased

struggling, then released and ingested, usually head first. Handling times increased with prey size.

The length at which 50% of Pacific mackerel larvae were capable of capturing and ingesting anchovy yolk-sac larvae (LD_{50}, Finney 1952) was 8.1 mm SL (95% confidence interval, 7.2-9.5 mm) (Figure 6). Sibling cannibalism began when the mean length of the group was about 8 mm SL. At this size, the mean length of six cannibals was 10.8 mm SL (range 9.9-12.0 mm) and that of their prey was 6.2 mm SL (range 5.9-6.5 mm). Cannibalism in rearing containers ended as Pacific mackerel approached metamorphosis (15 mm SL) and schooling began. Rearing at higher temperatures increased the growth rate and thereby decreased the period over which sibling cannibalism occurred. Consequently, survival at metamorphosis was higher in groups reared at 20°-22° C (5-6%) than it was at 19° C or lower temperatures (1-2%).

Near metamorphosis, Pacific mackerel were able to eat relatively large fish larvae. Three Pacific mackerel, 15.4-16.0 mm SL, placed in a rearing tank with northern anchovy larvae (12.0-20.6 mm SL) captured and began to ingest larvae of 11.7-13.5 mm SL, within 6 min. Thus, as Pacific mackerel larvae grew from 8 mm SL to metamorphosis, the size of anchovy larvae, they were able to eat increased from about 3 to 13 mm SL. This increase in prey size was not closely related to mouth size of the Pacific mackerel because the mouth can be greatly expanded when ingesting a larval fish. Mouth size probably was inversely related to handling time as in the case for adult fishes (Kislalioglu and Gibson 1976).

When prey are engulfed rather than seized, mouth size may give a good indication of the size of prey a larvae is capable of ingesting. The relation between mouth width and length in Pacific mackerel larvae was slightly curvilinear, and mouth width increased from 0.216 mm for first-feeding larvae (3.6 mm SL) to 0.987 mm at metamorphosis (15 mm SL) (Figure 7).

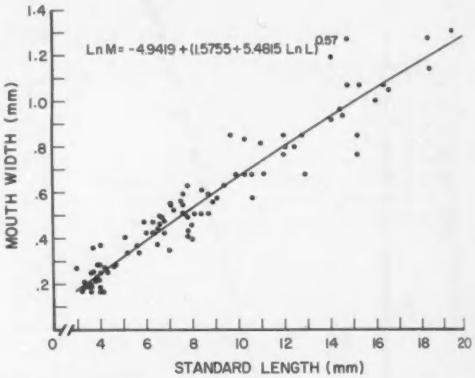

FIGURE 7.—Mouth width as a function of standard length of Pacific mackerel larvae. Points represent single larva.

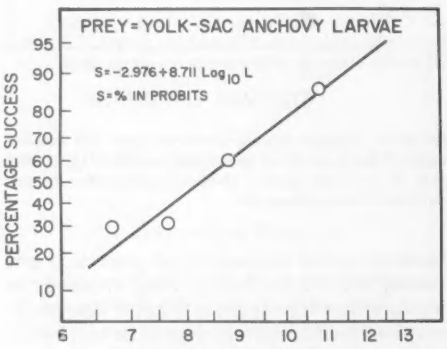

FIGURE 6.—Percentage of Pacific mackerel larvae (probit scale) that captured one or more yolk-sac anchovy larvae in relation to standard length of the mackerel (log_{10} scale). The length class was variable. Larvae were ranked by length and classes set at 10 observation intervals. The LD_{50} was 8.1 mm (95% confidence interval 7.2-9.5 mm).

The threshold, in terms of length for feeding on *A. salina* nauplii, was distinctly different from that for feeding on anchovy eggs. The 50% threshold for nauplii was 4.5 mm SL (95% confidence interval, 4.1-4.8 mm) and that for eggs was 12.2 mm SL (11.3-13.1 mm). This could be expected because anchovy eggs are nearly three times as large as *A. salina* nauplii. On the other hand, when feeding success was expressed as a function of the ratio, mean prey width/mean mouth width, the percentage feeding success of Pacific mackerel fed *A. salina* was similar to that of larvae fed eggs (Figure 8). At first feeding, relative prey size (prey width/mouth width) was near unity for larvae fed either *A. salina* or eggs, indicating the width of the mouth established the upper size limit of prey. Since the 50% threshold for relative prey size for the combined data given in Figure 8 was 0.85 (95% confidence interval,

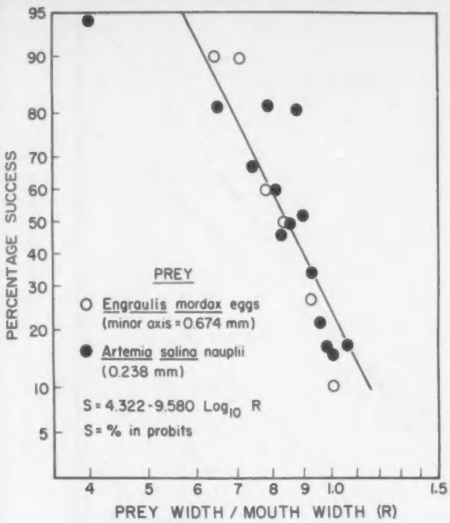

FIGURE 8.—Relation between average feeding success (probit scale) and average relative prey size (prey width/mouth width), for larval groups fed *Artemia salina* nauplii (closed circles) and northern anchovy eggs (open circles). Each point is the percentage success of fish within a mouth width/prey size class, where $n>9$. Line is the regression of percentage success probit on $\log_{10}$ of the prey-width to mouth-width ratio, for *A. salina* nauplii and anchovy egg data combined. The LD_{50} for the combined data was 0.85 (95% confidence interval 0.79-0.91).

0.79-0.91) and the 95% threshhold was 0.57 (0.47-0.70), nearly all Pacific mackerel larvae (95%) were able to ingest a prey when it was 57% of the width of the mouth and 50% were able to do so when it was 85% of the mouth width.

Nearly all prey eaten by Pacific mackerel larvae in the sea fell within the range of sizes predicted from the laboratory work; few prey exceeded the width of the mouth (Figure 9). Fifty-nine percent of all identifiable food items in the stomachs of sea-caught larvae were stages of copepods; other items included cladocerans, oikopleurans, gastropods, invertebrate eggs, diatoms, fecal pellets, and one fish larvae.

Although laboratory data indicated that 50% of Pacific mackerel larvae were able to ingest prey having a width of 85% of the mouth width, the mean diameter of prey eaten in the sea was 38±2% (2 SE) of the mouth width. Thus, a substantial number of prey eaten by larvae in the sea was much smaller than the maximum size of prey they were capable of ingesting. This may reflect a shortage of larger prey in the sea. Larger prey probably are important nutritionally. If one assumes the prey given in Figure 8 to be spherical, then 50% of the prey items accounted for about 85-90% of the total volume of food, depending on larval size. Conversely, the small prey items that contributed 50% by number, contributed only 10-15% of the total volume of prey eaten. This calculation underestimates the volume of the larger prey because they are more elongate or less spherical than smaller ones. Nevertheless, it indicates that prey less than the mean size eaten contributed relatively little nutritionally to the diet of Pacific mackerel larvae, and that the relatively large, but more rare, prey probably made the major contribution to growth.

Ration, Growth Efficiency and Metabolism

Pacific mackerel larvae (age 3-5 d) fed actively throughout the day; the gut was filled within the first hour of feeding and it remained full throughout the remainder of the 12-h feeding day, despite a high rate of gastric evacuation. Evacuated *Brachionus plicatilis* were well digested; only the lorica remained after digestion. Our measurements of evacuation rates indicated that about half the gut contents was evacuated in 2 h (Figure 10). Growth of larvae used for ration estimates was about the same as that for other groups reared at 19° C (Figure 3). To grow at this rate in the laboratory, Pacific mackerel larvae (age 3-5 d) consumed an average of about 87% of their dry body weight per day, or about 165-538 rotifers/day (Table 3). This estimate of ration was based on the dry weight of the mean number of rotifers in stomachs, adjusted for the rate of evacuation (Stauffer 1973). The mean gross growth efficiency in dry weight was 33%, which falls within the range of estimates for fish larvae and young fishes (Pandian 1967; Stepien 1976).

Our respiration experiments indicated that Pacific mackerel larvae at 18.0° C consumed 6.1±1.4 (2 SE) μl O_2/mg per h (n = 24) and at 22.0° C they consumed 11.4±3.0 μl O_2/mg per h (n = 14). By interpolation, the rate at 19° C, the temperature of the ration experiments, is estimated as 7.4 μl O_2/mg per h. This metabolic expenditure, converted to calories per day (footnote 6, Table 3) was, on the average, about 18% of the mean daily ration for larvae given in the table. This is probably an underestimate of their metabolic requirement because the activity of larvae confined in

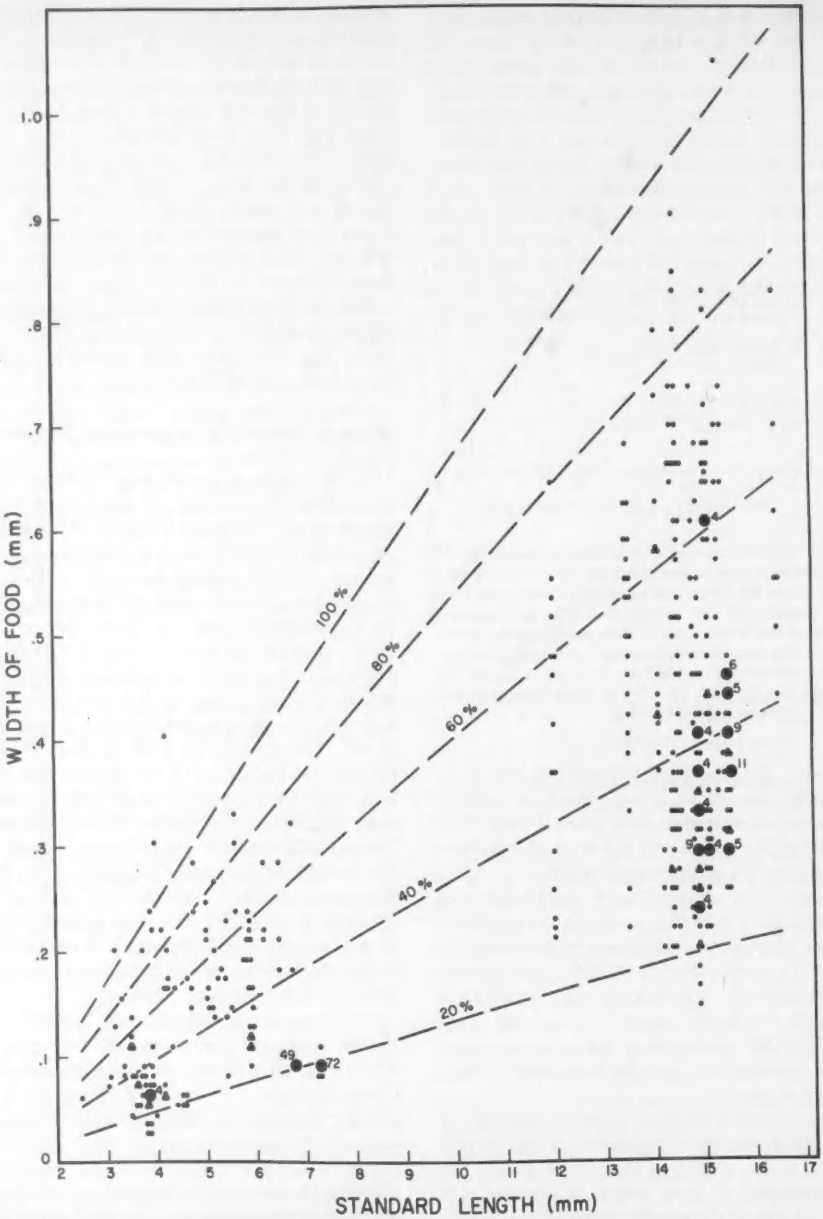

FIGURE 9.—Width of foods eaten in the sea by Pacific mackerel larvae of various standard lengths. Each small point is the width of a single prey; larger points represent multiple points for prey of the same size and number observations. Dashed lines indicate the prey width equal to 20-80% of the mouth width, or equal to the mouth width (100%), for Pacific mackerel larvae of 3-16 mm (calculated from data given in Figure 7).

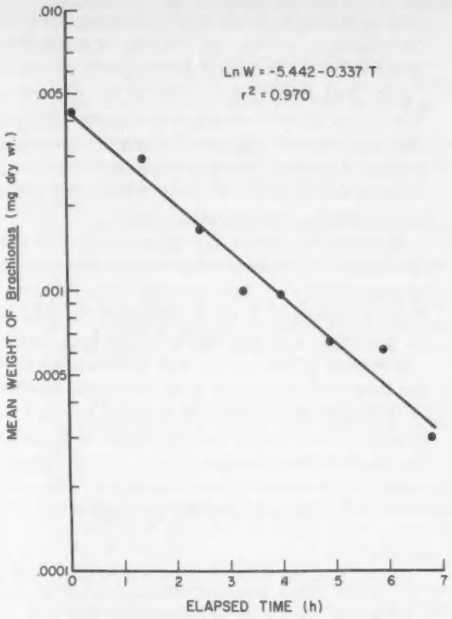

FIGURE 10.—Rate of gastric evacuation of 4.01±0.03 mm SL Pacific mackerel larvae fed *Brachionus plicatilis*. Each point represents the mean dry weight of *B. plicatilis* in guts of 13-16 larvae. Dry weight estimated by counting numbers of *B. plicatilis* in stomachs and multiplying by the mean dry weight of one *B. plicatilis* (0.16μg) (Theilacker and McMaster 1971).

Warburg flasks was probably less than that of free-swimming larvae. These respiration measurements do establish a lower limit to food ration, because the ration would have to exceed the metabolic requirement just to meet maintenance costs.

DISCUSSION

The characteristics of the embryonic period (duration of incubation and yolk-sac periods, extent of yolk reserves, size at first feeding, and ability to withstand starvation) were similar to other temperate fishes with small pelagic eggs (Lasker et al. 1970; Zweifel and Lasker 1976) and did not differ greatly from some subtropical species (Houde 1974). Small differences in these characteristics may be of importance (Houde 1974) but growth, metabolism, feeding, and swimming behavior are of more value in characterizing the early life history of Pacific mackerel.

Pacific mackerel larvae grew rapidly, completing metamorphosis (15 mm SL) in 2-3 wk. Fast growth appears to be characteristic of scombroid larvae and is even more rapid in tropical scombroids: *Auxis thazard* grew to 64 mm SL in 17 d (Harada, Murata, and Furutani 1973) and *A. tapeinosoma* grew to 49 mm SL in 18 d (Harada, Murata, and Miyashita 1973). Fast growth requires a large food ration; we found that Pacific mackerel larvae consumed about 87% of their dry

TABLE 3.—Estimate of ration, metabolism, and growth efficiency of 3-5 d old Pacific mackerel larvae fed *Brachionus plicatilis*.

Larval age (d)	Temperature (°C)	Larval SL±2 SE (mm)	Experimental conditions: Larval weight[1] On day of ration estimation (μg)	Gain 1 d after estimation (μg)	Food density (no./ml)	Mean weight in stomachs[2] No. of samples[3]	$\bar{x}$ ±2 SE (μg)
3	18.7	3.66±0.03	37.8	5.2	157	7	4.8±0.8
4	19.0	3.76±0.02	43.0	14.0	47	8	6.9±1.0
5	19.4	4.38±0.08	84.6	37.5	198	7	15.6±4.5
$\bar{x}$	19.0	3.93	55.1	18.9	134		9.1

Larval age (d)	Ration[4] μg/d	Ration[4] Percent body weight/d	Ration[4] [5]cal/d	Metabolic rate[6] (cal/d)	Weight gain[7] (cal)	Gross growth efficiency[8] (percentage)
3	26.5	70	0.141	0.0338	0.026	20
4	38.1	89	0.203	0.0384	0.070	37
5	86.2	102	0.460	0.0756	0.188	44
$\bar{x}$	50.3	87	0.268	0.0493	0.094	33

[1]Calculated from mean larval length using relation given in Figure 4.
[2]Mean counts of *B. plicatilis* in stomach converted to weight using one *B. plicatilis* = 0.16 μg (Theilacker and McMaster 1971).
[3]Each sample consisted of 13-16 larvae; sampling began after first hour of feeding.
[4]Ration = $(r \times k \times t) + r$, where r is mean stomach contents, k is rate of gastric evacuation (0.377), and t is duration of feeding period (12 h). (From G. Stauffer, unpubl. manuscr., Southwest Fisheries Center, La Jolla, Calif.)
[5]Caloric value of *B. plicatilis* = 5,335 cal/g (Theilacker and McMaster 1971).
[6]Maintenance requirement from: 7.45 μl O_2/mg per h; 1 μl O_2 = 0.005 cal; time = 24 h; and dry weight of larvae on day ration estimated.
[7]Caloric value of weight gained assumed to equal 5,000 cal/g.
[8]Gross efficiency (dry weight) = weight gain/ration.

weight per day and weight increased from 0.034 mg to 7.5 mg over the larval period. To capture sufficient numbers of prey to support such rapid growth requires that the size of the prey and the size of the mouth increase rapidly. Our analysis of sea-caught Pacific mackerel larvae showed that the maximum size of prey did increase rapidly, more or less, in proportion to mouth size. The mean and minimum size of prey eaten by Pacific mackerel changed more slowly but the smaller prey, those less than the average size, may constitute <15% of the volume of food eaten. A similar pattern of rapidly increasing prey size with length also has been documented for *Scomber japonicus* larvae by Shirota (1970) and Yokota et al. (1961).

A dependency on larger prey and fast growth requires faster swimming to increase the volume of water searched for prey because abundance declines with increased prey size (Sheldon et al. 1972). The swimming behavior of Pacific mackerel larvae appeared consistent with this argument. Cruising speeds increased rapidly with length, roughly to the 1.8 power, and speeds of the larger larvae were at the upper end of the range, typical of larval fishes (3 SL/s) (Blaxter 1969). Higher speeds require a greater metabolic expenditure. The rate of oxygen consumption for Pacific mackerel (6-11 μl O_2/mg per h) was above that for other marine fish larvae (Blaxter 1969) indicating a higher-than-average metabolic expenditure despite the fact that the rates probably do not reflect the entire cost of high speed swimming.

Piscivorous feeding was an important behavioral trait in the early life history of Pacific mackerel because larvae were no longer limited to prey sizes equal to or less than the size of an open mouth. In piscivorous feeding, prey were seized, manipulated and the mouth greatly expanded during ingestion, permitting consumption of much larger diameter foods. In our samples of sea-caught larvae, only one stomach contained a larval fish, but the actual incidence may be higher because larvae are digested rapidly. Cannibalism, a correlate of piscivorous feeding, was common in laboratory groups after the larvae reached 8 mm SL. This also has been observed from stomach contents of the Atlantic mackerel, *S. scombrus* (Lett 1978). Cannibalism appears to be a common feature of scombroid life history; Mayo (1973) remarked that *Euthynnus alletteratus*, *Scomberomorus cavalla*, *S. regalis*, and *Auxis* sp. became cannibalistic at about 5 mm SL. He also noted that cannibalism ceased as the fish became juveniles which agrees with our observation that cannibalism ended as Pacific mackerel approached metamorphosis and began to school. The extent that cannibalism affected the form of our laboratory growth curves is unknown. Although cannibalism was high in all groups, survival was higher in groups reared at high temperatures because of the faster growth rate, which meant faster transit through cannibalistic sizes.

In summary, traits that characterize the early life history of Pacific mackerel are the interrelated characteristics of fast growth, fast swimming, high metabolism, a dependence on increasingly larger prey, and cannibalism. The high food requirements of the larvae, and the fact that in the sea they feed upon many prey substantially smaller than they are capable of eating, indicates that growth or survival in the sea might be limited by the availability of larger prey.

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SPAWNING AND FECUNDITY OF ATLANTIC MACKEREL, *SCOMBER SCOMBRUS*, IN THE MIDDLE ATLANTIC BIGHT

WALLACE W. MORSE[1]

ABSTRACT

Collections of Atlantic mackerel, *Scomber scombrus*, were made during spring 1977 from Maryland to Rhode Island. Length-weight relationships were determined for total and fork lengths and total and gutted weights. Spawning time was determined from gonad somatic indices and peak spawning occurred between 21 April and 4 May. Egg diameter frequencies from running ripe ovaries indicated five to seven egg batches are spawned by each female during the spawning season. Fecundity was estimated and ranged from 285,000 to 1,980,000 for fish between 307 and 438 mm fork length. Fecundity was related to fork length, gutted weight, and age.

The Atlantic mackerel, *Scomber scombrus* Linnaeus, is a schooling, pelagic species ranging from the Gulf of St. Lawrence to North Carolina in the northwest Atlantic and from Norway to Spain in the northeast Atlantic. The northwest Atlantic population has been separated into northern and southern contingents on the basis of size composition, spawning times, summer distributions, and tagging studies (Sette 1950; Moores et al. 1975; MacKay[2]).The northern contingent spawns in the southern Gulf of St. Lawrence from about the end of May to mid-August (Ware 1977). The southern contingent spawns from mid-April to June from North Carolina to Massachusetts (Berrien 1978).

Fecundity estimates of northwest Atlantic mackerel are limited to a few observations ranging from about 500,000 to 1,000,000 eggs (Brice 1898: 208-213; Sette 1943). Fecundity of northeast Atlantic mackerel ranged from approximately 130,000 to 1,100,000 eggs for fish 28.5-46.0 cm total length (Macer[3]; Lockwood[4]). This paper presents the results of a fecundity and spawning time investigation of the southern contingent.

METHODS

Atlantic mackerel were collected between 9 April and 21 May 1977 from recreational and commercial catches from Maryland to Rhode Island (Table 1). Length frequencies of males and females are shown in Figure 1. All fish were measured to the nearest millimeter fork length (FL) and total length (TL), and weighed to the nearest gram total weight (TW) and gutted or somatic weight (GW). Otoliths were extracted for age determination. Ovaries of all mature females were exsected, weighed to the nearest 0.01 g, and preserved in 10% Formalin.[5]

Preliminary observations of eggs from ovaries in the spawning condition revealed that three egg types were present: 1) small, translucent eggs; 2)

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[2]MacKay, K. T. 1973. Aspects of the biology of Atlantic mackerel in ICNAF Subarea 4. Int. Comm. Northwest Atl. Fish., Res. Doc. 73/70, 11 p.

[3]Macer, C. T. 1976. Observations on the maturity and fecundity of mackerel (*Scomber scombrus* L.) Int. Counc. Explor. Sea, CM 1976/H:6, 7 p.

[4]Lockwood, S. J. 1978. The fecundity of mackerel, *Scomber scombrus* L. Int. Counc. Explor. Sea, CM 1978/H:9, 5 p.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Catch data of Atlantic mackerel sampled in 1977.

Date	Port	Numbers of fish examined		Capture method
		Female	Male	
9 April	Ocean City, Md.	16	8	Otter trawl
16	Cape May, N.J.	15	10	Hook and line
20	Ocean City	26	26	Otter Trawl
25	Barnegat, N.J.	20	25	Hook and line
27	Greenport, N.Y.	64	36	Pound net
28	Belford, N.J.	10	15	Otter trawl
28	Sheepshead Bay, N.Y.	6	16	Hook and line
30	Sheepshead Bay	9	12	Hook and line
1 May	Sheepshead Bay	6	17	Hook and line
4	Barnegat	16	36	Hook and line
5	Barnegat	39	66	Hook and line
7	Sheepshead Bay	11	19	Hook and line
8	Point Pleasant, N.J.	17	8	Hook and line
9	Point Judith, R.I.	42	43	Otter trawl
11	Belmar, N.J.	5	20	Hook and line
14	Sheepshead Bay	12	38	Hook and line
15	Sheepshead Bay	4	33	Hook and line
17	Sandy Hook, N.J.	22	20	Hook and line
18	Point Judith	32	48	Otter trawl
22	Sheepshead Bay	77	21	Hook and line
Totals		449	517	

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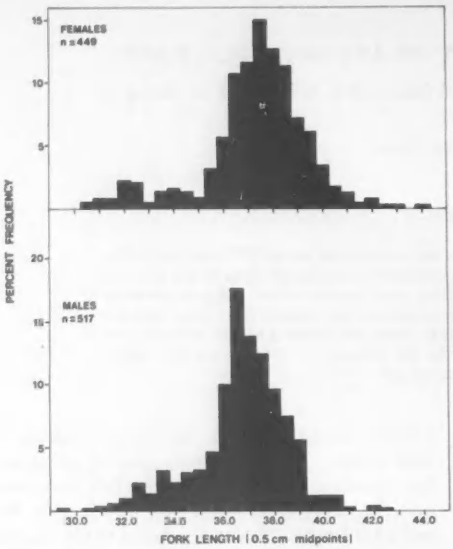

FIGURE 1.—Length frequencies of male and female Atlantic mackerel used in this study.

larger opaque, yolked eggs; and 3) large translucent eggs. There appeared to be no clear size separation between egg types, which is indicative of serial spawners (Hickling and Rutenberg 1936). Therefore, the method described by Hislop and Hall (1974) for whiting, *Merlangus merlangus*, was used to determine which eggs would be shed during the current spawning season. Since yolk deposition indicates eggs are ripening for spawning, random samples of 300 eggs were measured from ovaries at successive maturity stages to determine the average minimum size of yolked eggs. Eggs 0.20 mm and larger contained yolk and were included for fecundity estimation. Ovaries were classified into four maturity stages based upon macroscopic examination and the occurrence of mature eggs (Table 2). Egg diameter frequencies of yolked eggs from ovaries in the developing, ripe, running ripe, and partially spent condition are shown in Figure 2.

Ovaries in the ripe condition (Figure 2b) were used for fecundity estimations. If large translucent eggs (1.00-1.35 mm) were present in the lumen of the ovary, which is indicative of the running ripe condition (Figure 2c), the ovary was not utilized for fecundity because some eggs may have been shed and fecundity would be underestimated.

TABLE 2.—Maturity stages of Atlantic mackerel ovaries.

Stage	Description
1. Developing	Ovary enlarged, usually orange colored with a granular appearance. No translucent eggs, maximum egg diameters 0.8-0.9 mm.
2. Ripe	Ovary fills most of gut cavity, yellow colored, in advanced stage some translucent eggs are visible through wall. Maximum egg diameter 1.0-1.2 mm.
3. Running ripe	Similar in appearance to stage 2, eggs are extruded with pressure on abdomen of fish. Maximum egg diameters 1.2-1.4 mm.
4. Partially spent	Ovary is flaccid, often hemorrhaging is evident at anterior portion of ovary, some residual mature eggs (1.1-1.4 mm) present.

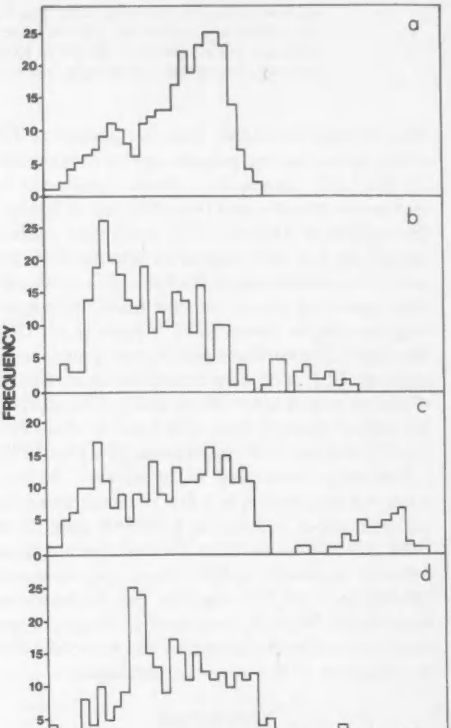

FIGURE 2.—Egg diameter frequencies of Atlantic mackerel ovaries in stages: developing (a), ripe (b), running ripe (c), and partially spent (d). Each graph based on 300 egg measurements.

Suitable ovaries were removed from the Formalin solution, placed in glacial acetic acid for 5 min, and washed, and the eggs were separated with a gentle

stream of water and agitated in a 0.20 mm mesh sieve. Following removal of the ovarian tissue, the eggs were air dried on blotter paper for 2-3 min and weighed (±0.01 g), and two subsamples were removed and weighed (±0.01 mg). All eggs in each subsample were counted and the mean used to calculate total egg numbers based on the weight of all eggs in the ovary. If the two subsample counts differed by 10% or more, additional samples were taken until two counts differed by <10%.

Ages were determined from otoliths as described by Steven (1952).

RESULTS

The allometric relationships of length-weight were expressed by the power function:

$$Y = aX^b \qquad (1)$$

where X is length, Y is weight, and a and b are constants. Equation (1) was converted to the linear form by a logarithmic (base 10) transformation to:

$$\log Y = \log a + b \log X\,. \qquad (2)$$

The interrelationships between length measurements and between weight measurements were expressed by the linear function:

$$Y = a + bX \qquad (3)$$

where Y and X are both length or both weight. All data were fitted using least-squares regression techniques.

Predictive regression equations were calculated using all observations for males and females and an analysis of covariance applied to determine possible sex related differences. No significant differences ($P = 0.05$) were indicated between sexes and sexes were therefore pooled. The pooled regression equations and associated statistics are presented in Table 3.

To determine the peak spawning time the mean gonad somatic index (GSI = percent ovary weight of the gutted weight) was calculated for each week of the sampling period (Figure 3). It appears that individual fish attain their maximum GSI just prior to spawning the first egg batch and a decline in GSI occurs as successive batches are spawned. This was shown by comparing the mean GSI of each maturity stage (Table 4) which showed an increase from stage 1 to 3 and a rapid decrease at stage 4. Similar results were reported by Kaiser (1973) for horse mackerel, *Trachurus murphyi*. He found that gonad somatic indices reflected maturation changes of the ovaries and a sharp decline in the mean GSI coincided with the appearance of the earliest spawning females. In this study the weekly mean GSI increased during the first 3 wk of sampling, peaked between 21 April and 4 May, and then declined steadily through the end of the sampling (22 May). All females examined from the last sampling week were partially spent and indicated spawning was nearly completed within the study area.

TABLE 3.—Length and weight relationships of Atlantic mackerel collected in the Middle Atlantic Bight, 1977. TW = total weight (grams); GW = gutted weight (grams); TL = total length (millimeters); and FL = fork length (millimeters). Symbols refer to the equation $Y = a + bX$; n = sample size; r = correlation coefficient; $S_{y.x}$ = standard deviation about the line.

Y	a	b	X	n	r	$S_{y.x}$
Curvilinear relationships between transformed variates						
log TW	-5.767	3.275	log TL	966	0.905	0.036
log GW	-5.420	3.106	log TL	966	0.924	0.030
log TW	-5.780	3.334	log FL	966	0.905	0.036
log GW	-5.374	3.140	log FL	966	0.924	0.030
Linear relationships between untransformed variates						
TL	1.793	1.098	FL	966	0.986	3.594
TW	-20.410	1.282	GW	966	0.979	22.397

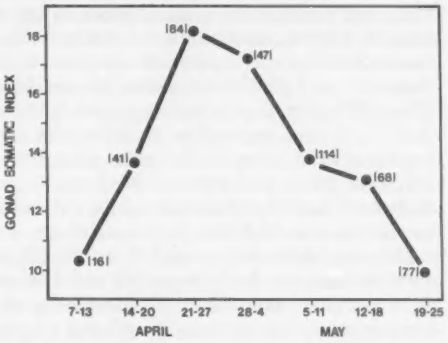

FIGURE 3.—Mean gonad somatic index (ovary weight as a percent of gutted weight) plotted by week for Atlantic mackerel sampled in 1977. Numbers in parentheses are sample sizes.

TABLE 4.—Mean gonad somatic index (GSI) and standard deviation for each maturity stage of Atlantic mackerel.

Stage	Mean GSI	SD	n
1. Developing	10.4	2.9	68
2. Ripe	15.0	4.2	247
3. Running ripe	24.9	4.7	41
4. Partially spent	8.6	2.2	93

The egg diameter frequencies shown in Figure 2 indicate Atlantic mackerel are serial spawners, i.e., several batches of eggs are shed by individuals throughout the spawning season. The presence of multiple modes in the egg diameter frequencies (Figure 2a-c) and ripening eggs in partially spent ovaries (Figure 2d) are indicators of serial spawning (Clark 1935; MacGregor 1957). A cytological study by Bara (1960) has shown that eggs are not shed continuously as stated by Cunningham (1889) but are shed in several batches during the 2-mo spawning period.

The potential number of batches spawned was estimated by determining the ratio of ripe eggs to all yolked eggs in six running ripe ovaries. Atlantic mackerel eggs, from plankton samples, ranged from 1.01 to 1.29 mm diameter (Berrien 1975; Ware 1977); therefore, in this study, eggs 1.05 mm and larger were assumed to constitute the next egg batch to be spawned. The ratios ranged from 13.7 to 21.7% and averaged 17.0%. Thus the potential number of batches spawned per individual was five to seven and averaged six batches.

Fecundity estimates ranged from 285,000 to 1,980,000 eggs for fish between 307 and 438 mm FL. Preliminary plots indicated a curvilinear relationship existed for fecundity-length and a linear relationship for fecundity-weight and fecundity-age. However, correlation coefficients (r) were higher for the logarithmic relationships of fecundity-weight and fecundity-age, therefore, all variables were transformed and linear regression equations of the form $\log Y = a + b(\log X)$ were calculated. Data plots and the equations relating fecundity to fork length, gutted weight, and age are shown in Figures 4-6.

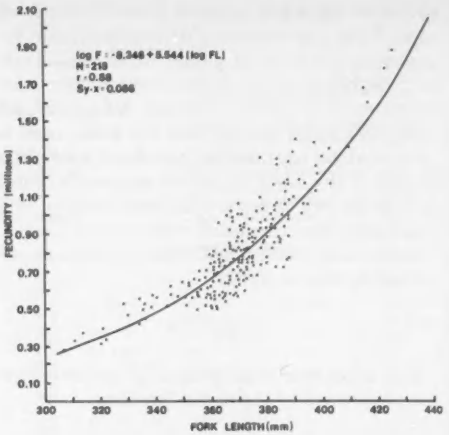

FIGURE 4.—Relationship of fecundity and length and the predictive logarithmic (base 10) regression for Atlantic mackerel in 1977.

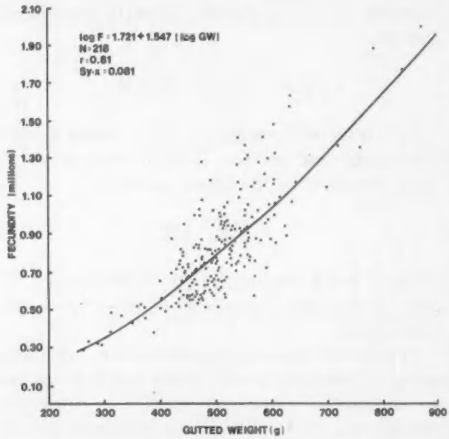

FIGURE 5.—Relationship of fecundity and weight and the predictive logarithmic (base 10) regression for Atlantic mackerel in 1977.

DISCUSSION

Spawning by the southern contingent of Atlantic mackerel apparently peaked during the 2-wk period between 21 April and 4 May 1977. This 2-wk period represents the mean peak spawning time within the study area (Maryland to Rhode Island) since there is a north and eastward progression of spawning during the spring migration (Bigelow and Schroeder 1953; Berrien 1978). Berrien et al.[6] observed the north and east progression in plankton mackerel egg densities. They found spawning intensity in the Middle Atlantic Bight was low during mid-April and increased rapidly by late April, and maximum egg densities occurred about 25 April. Spawning continued at a reduced rate throughout May and then decreased steadily during June. Very similar results are indicated from my analysis of gonad somatic indices during the 1977 spawning season.

[6]Berrien, P. L., A. Naplin, and M. R. Pennington. 1979. Atlantic mackerel, *Scomber scombrus*, egg production and spawning population estimates for 1977 in the Gulf of Maine, Georges Bank, and Middle Atlantic Bight. Int. Counc. Explor. Sea ICES/ELH Symp./DS:9, 17 p.

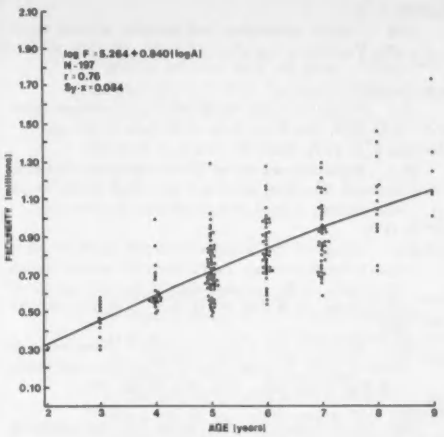

FIGURE 6.—Relationship of fecundity and age and the predictive logarithmic (base 10) regression for Atlantic mackerel in 1977.

Observations of spawning times of various temperate-water fish have indicated peak spawning dates may be relatively fixed. Cushing (1969) postulated an indirect link between the fixity of spawning season and the primary production cycle. Ware (1977) investigated the relationship of spawning time of Atlantic mackerel at St. Georges Bay, Nova Scotia, to the size and abundance of 80 μm plankton. He found the mean peak egg production date was 1 July ± 1 wk and coincided with the maximum abundance of summer plankton. It would appear, at least for the southern contingent, that the time of peak spawning is more variable than that indicated for St. Georges Bay. Sette (1943) determined maximum spawning occurred during mid-May (1928-32) off Middle Atlantic and southern New England States. Ichthyoplankton surveys during the mackerel spawning season in 1966 and 1975-77 (Berrien 1978; Berrien et al. see footnote 6; Berrien and Anderson[7]) within the Middle Atlantic Bight indicated spawning peaked during May in 1966 and 1975 and during April in 1976 and 1977. In fact, eggs were collected as early as 13 April in 1977. Berrien and Anderson (see footnote 7) attribute the April 1976 spawning peak to increased water temperatures within the study area.

The factors controlling the spawning time of Atlantic mackerel are unclear. The regularity shown by Ware (1977) would indicate internal control or a constant external stimulus such as photoperiod. Sette (1943) presented evidence indicating water temperature is a limiting factor controlling migration and in turn the timing of spawning in a fixed location. Cushing (1967, 1969) suggested that some fish spawn at a relatively fixed date that is linked to planktonic productivity and that changes in plankton production would cause dramatic changes in year-class success. It appears that a variable spawning date, as shown by the southern contingent—linked to the factors affecting plankton productivity, e.g., temperature, photoperiod, nutrient content—would increase the chances for larval survival.

The fecundity estimates presented here must be considered as maximum potential egg production because, as reported by Macer (see footnote 3), resorption may significantly reduce the number of eggs spawned. Preliminary observations by Macer indicated an average of 11.4% of yolked eggs were being resorbed. Bara (1960) observed degeneration in a "few" mature eggs though no quantitative data were presented. Studies are needed to define the extent and possible annual changes of resorption rates and their relationship to fecundity.

ACKNOWLEDGMENTS

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RESPIRATION AND DEPTH CONTROL AS POSSIBLE REASONS FOR SWIMMING OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, YOLK-SAC LARVAE

DANIEL WEIHS[1]

ABSTRACT

Larval northern anchovy in the yolk-sac (nonfeeding) stage exhibit regular bursts of continuous swimming during the first 3 days after hatching. It has been suggested that this behavior may have a respiratory function. A different possibility is depth control, countering the tendency of the larvae to sink when motionless. This paper includes a theoretical and experimental investigation of the possible functions of these swimming bouts.

The theoretical approach was to define a model and calculate the oxygen available to the larva when resting and while moving, and experiments were performed as a check of the theoretical results. The experiments were conducted on yolk-sac larvae in sealed tanks with varying dissolved oxygen concentrations to determine the effects of reducing the available oxygen on the frequency and duration of the swimming bursts. Results of the experiments confirmed the theoretical model. They indicate that the swimming bouts both help the larva stay at a constant depth and have a respiratory function when the oxygen concentration in seawater is less than 60% of saturation.

Newly hatched northern anchovy, *Engraulis mordax*, larvae exhibit a pattern of regular short bouts of continuous swimming interspersed with periods of resting. These larvae are still in the yolk-sac stage and are not feeding so that the locomotory behavior must have some other purpose, as these motions are energy consuming and also endanger the animal by attracting predators (Lillelund and Lasker 1971). Hunter (1972) suggested that these swimming bouts might have a respiratory function. Respiration has to be by cutaneous diffusion through the 2-3 μm thick skin (Lillelund and Lasker 1971) of the larvae as the gills develop only at a later stage. The purpose of this paper is to test this hypothesis and another possibility, depth control, to counter sinking due to the negative buoyancy, using theoretical and experimental methods.

First, I develop a theoretical model for oxygen transport to motionless and swimming yolk-sac larvae and estimate the possible oxygen uptake. Next, I describe the experiments to test the prediction of the theory for both proposed mechanisms and compare their results.

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METHODS

Analytical Model

A mathematical model is now introduced to consider the possible respiratory function of the bouts of continuous swimming of yolk-sac anchovy larvae. First, we calculate the oxygen transport to a motionless larva. This transport is then compared with the metabolic requirements. If the metabolic requirements are not met, larval motion (and the resulting convective diffusion) is required.

The size of yolk-sac larvae (2.7-4.0 mm total length) and their swimming speeds (Hunter 1972) lead to typical Reynolds numbers, based on larval length (Weihs 1980) of <20. (The Reynolds number is a nondimensional factor indicating the relative importance of pressure and viscous effects on a body moving in a fluid under given circumstances—the higher the Reynolds number, the smaller the influence of the viscosity.) The larvae, as a direct result of their small size, are in a highly viscous laminar flow situation in which turbulent effects can be neglected. Thus, the larvae and their immediately surrounding water would be transported together in oceanic turbulent eddies, which are of the order of tens of centimeters in diameter. As a result, a nonswimming larva would stay for a relatively long period in the same mass

of water, even though that mass is convected on a much larger scale.

The motionless larva and its surrounding water mass may therefore be analyzed separately, as a distinct system in the thermodynamic sense. Within this system, oxygen transport to the larva is controlled by molecular diffusion because the gill system is not developed at this stage. This process is time dependent, beginning when the larva arrives in a certain location (by swimming) and rests, ending when swimming begins again. Initially the oxygen concentration in the water mass surrounding the larva is uniform, but the larva now starts acting as an oxygen sink, gradually depleting the oxygen content of the water surrounding it. This concept of the larva as an oxygen sink simplifies the calculations, as knowledge of the exact distribution of oxygen diffusivity on the animal's surface is not required. The sink model also is useful here as it averages out the direction of local transport and the body of the larva into which the oxygen diffuses can be taken as an equivalent sphere of equal surface area (Figure 1).

Diffusion into a sphere is most conveniently analyzed in the spherical coordinate system. The governing conservation of mass equation can be written (Crank 1975) as

$$\frac{\partial c}{\partial t} = D\left(\frac{\partial^2 c}{\partial r^2} + \frac{2}{r}\frac{\partial c}{\partial r}\right) \tag{1}$$

where c is the mass fraction of oxygen (a function of the distance and time); r is the radial distance, measured for the center of the equivalent spherical body (the sink); t is the time; and D is the diffusion coefficient of oxygen in seawater.

The temporal boundary condition is the initial, uniform state

$$c(r, 0) = c_0 \tag{2}$$

while the spatial conditions are

$$c(\infty, t) = c_0 \tag{3}$$

which states that far from the animal the oxygen concentration stays unchanged at all times. Strictly, the condition should be defined at some finite distance but as that distance is much larger than the animal equivalent radius, it can be approximated by ∞. Next, the oxygen concentration boundary condition at the surface of the equivalent sphere $r = a$ is obtained. Muscles and vascularized tissues have much higher oxygen transport rates than seawater, due to internal uptake augmented by active transport. Thus, oxygen will be absorbed at the surface of the larva as fast as it arrives by diffusion from the surrounding water. The oxygen concentration c at the larva's surface ($r = a$) is thus constant, and very low, i.e.,

$$c(a, t) = c_1 \tag{4}$$

where $c_1 \to 0$ and $t > 0$.

Equations (2)-(4) enable solving equation (1) analytically, by classical methods. The solution can be written in nondimensional form for the concentration as

$$\frac{c - c_0}{c_1 - c_0} = \frac{a}{r}\,\mathrm{erfc}\,\frac{r - a}{2\sqrt{Dt}} \tag{5}$$

where the complementary error function, erfc, is defined as

$$\mathrm{erfc}(z) = \frac{2}{\sqrt{\pi}}\int_z^\infty e^{-z^2}\,dz\,. \tag{6}$$

Numerical values of the complementary error function are found in most mathematical tables (e.g., Abramowitz and Stegun 1965).

The rate of mass transfer (flux) J to the animal is now obtained from

$$J = -\rho D \int_A \frac{\partial c}{\partial r}\,dA \quad \text{(surface A)} \tag{7}$$

where ρ is the density and A the surface area of the body. For the equivalent sphere of radius a, $A = 4\pi a^2$. $\partial c/\partial r$ is assumed spherically symmetric so that

$$J = -\rho D A \left.\frac{\partial c}{\partial r}\right|_{r=a} \tag{8}$$

where the concentration derivative is obtained from Equation (5). Substituting this, and the value for the surface area, and setting $c_1 = 0$ as in Equation (4), the total mass flux per unit time J_d is

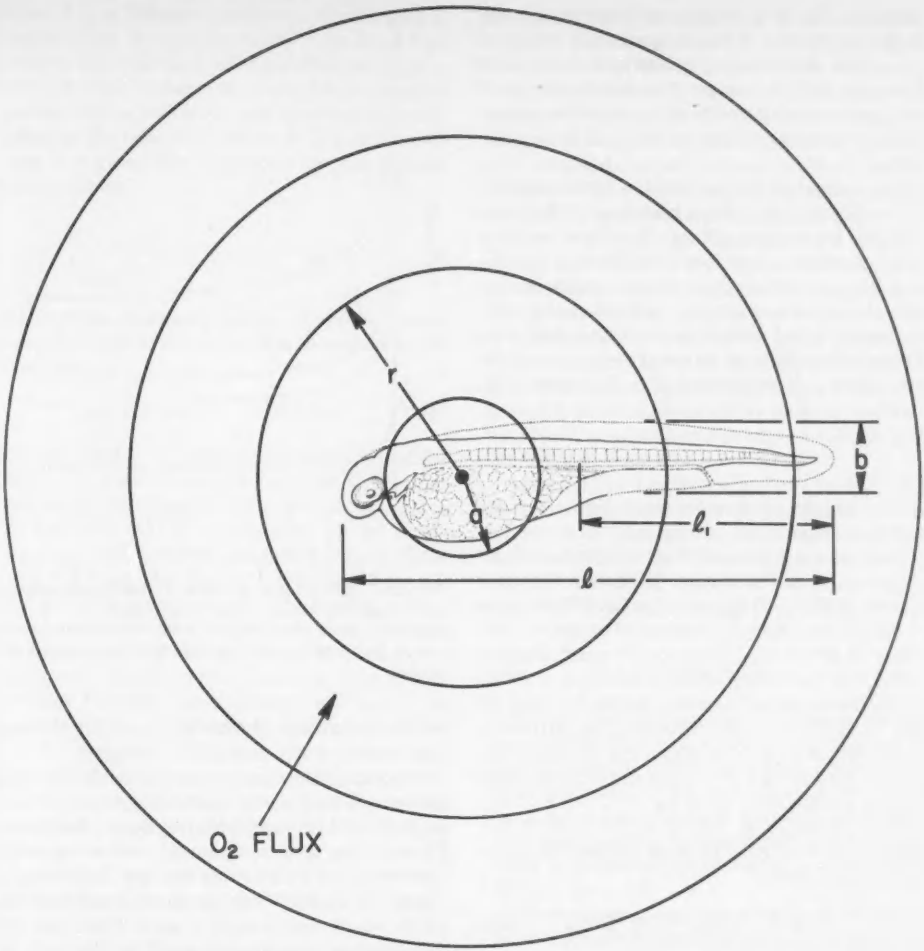

FIGURE 1.—Schematic description of model and spherical coordinate system centered on the center of mass of a northern anchovy larva: a is the radius of an equivalent sphere of equal surface area (not to scale), l is the larval length, and b and l_1 are the average tail strip depth and length.

$$J_d = -\rho D c_0 \cdot 4\pi r^2 \frac{a}{r} \operatorname{erfc}\left(\frac{r-a}{2\sqrt{Dt}}\right) \cdot \left(\frac{1}{2\sqrt{Dt}} + \frac{1}{r}\right) \qquad (9)$$

and when $r = a$, this simplifies to

$$J_d = 4\pi\rho D c_0 a^2 \left(\frac{1}{a} + \frac{1}{2\sqrt{Dt}}\right). \qquad (10)$$

Equation (10) consists of two terms in the brackets, multiplied by a constant factor. The first term in the brackets is the constant, time-independent contribution while the second describes the initial

transient. The latter drops rapidly, proportionally to the square root of time elapsed since arrival of the larva. Substituting numerical values into Equation (10), the oxygen flux can be compared with oxygen requirements of larval anchovy to see if the swimming motions are required for respiration.

The equivalent radius, a, of the larval anchovy is found by equating the surface area of the larva and the equivalent sphere. The larva, at this yolk-sac stage, is described for diffusion purposes as a sphere of radius q (the yolk sac) attached to an almost flat ribbon of length l_1 and average breadth b. The combined surface area of the sphere and ribbon is then taken to be equal to the area of the equivalent sphere appearing in Equation (10). Thus

$$4\pi a^2 = 2\, l_1\, b + 4\pi q^2. \qquad (11)$$

Using typical values for these parameters for newly hatched larvae we obtain $l_1 = 1.4$ mm, $b = 0.3$ mm, and $q = 0.3$ mm (from drawings by E. H. Ahlstrom, Senior Scientist, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038), i.e., $a = 0.0395$ cm. The mass content of oxygen in seawater at 20° C is $c_0 = 7.8 \times 10^{-6}$ g/cm³ (Prosser 1973), and the mass fraction is obtained by dividing by the density of seawater, which then cancels out in Equation (10). Finally, the diffusion coefficient of oxygen is approximately equal for freshwater and seawater (Riley and Skirrow 1965) so that a reasonable value for 20° C is 1.8×10^{-5} cm²/s (O'Brien et al. 1978), or $D = 1.08 \times 10^{-3}$ cm²/min. Substituting all these values into Equation (10) we obtain

$$J = (4.18 + 2.51\, t^{-1/2})\, 10^{-9}\ \text{g/min} \qquad (12)$$

when the water is 100% saturated. Reducing the oxygen content of the water causes the value of the oxygen flux, J, to go down proportionally, i.e., by multiplying J from Equation (12) by the fraction of saturation. Some typical values of J appear in Figure 2 with the percent of saturation as the parameter.

When the larva starts swimming, two changes in the oxygen supply occur. First, the animal's motion produces a convective local flow relative to the body, thus bringing new, oxygen-rich water closer and removing the respiratory waste products. Secondly, the absolute motion will bring the larva to an area where the oxygen concentration is still at the initial ambient value, starting the process described by Equations (1)-(4) again.

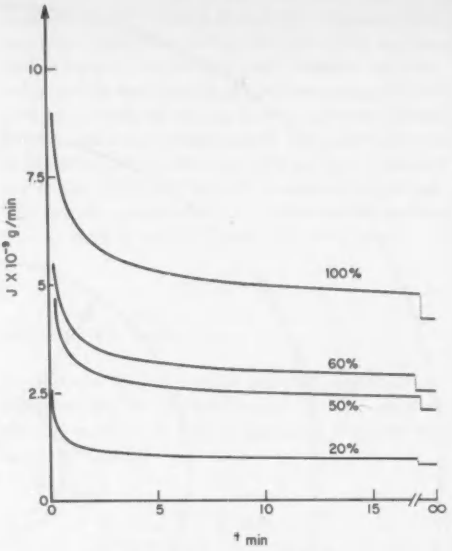

FIGURE 2.—Rate of oxygen transport (J) to motionless northern anchovy larva by diffusion versus time (t). Broken part of curve shows asymptotic value, after the initial transient has disappeared. Parameter is oxygen concentration in percentage of saturation.

Following this reasoning, even relatively slight motions causing just a local flow around the animal's body would suffice for respiratory functions. Thus, actual swimming would not be required. However, the yolk-sac larvae are increasingly negatively buoyant with age (Hunter and Sanchez 1976), which causes them to sink. Therefore, active absolute motion is necessary for the larva to stay at a given depth for feeding and future schooling.

When the larva is swimming, the process of transport of oxygen changes to convective diffusion, and as such is described by a different model (Daykin 1965). Daykin's work dealt with stationary eggs in a moving river environment, but for mass transfer purposes this is equivalent to a larva (or egg) moving at constant speed relative to the water. In the convective diffusion process (Levich 1962; Daykin 1965), the mass transfer to the larva can be roughly described by

$$J_{con} = 4\pi a^2 (c_0 - c_1) k \qquad (13)$$

where k is a diffusion coefficient obtained from experimental correlations of the diffusional flux with the Reynolds (Re) and Schmidt numbers (Sc). (The Schmidt number is the ratio of the kinematic viscosity to the diffusivity and nondimensionally indicates the relative importance of these two effects in a given flow situation.) For the present circumstances

$$k = \frac{D}{2a}(2 + 0.6\,\mathrm{Re}^{1/2}\,\mathrm{Sc}^{1/3}) \qquad (14)$$

for average swimming speeds of approximately 5 cm/s (Hunter 1972) and a Schmidt number of 600 we have

$$J_{con} = 1.27 \times 10^{-7}\ \text{g/min}. \qquad (15)$$

Hence, oxygen transport due to convective diffusion is over 20 times higher than for the motionless larva (Equation (12)). The calculation leading to Equation (15) is approximate, as the larva's shape will influence the coefficient 0.6 in k (Equation (14)) and also change the form of Equation (13). It is, however, accurate to at least an order of magnitude (Levich 1962). Thus, once the larva starts swimming, the mass transfer of oxygen to its surface increases by at least an order of magnitude. Recently, an additional mechanism for oxygen transport to stationary eggs was identified by O'Brien et al. (1978) who showed that under certain riverbed conditions natural convection, due to the oxygen and metabolite gradients, may contribute to the oxygen transfer. This effect may play a supplementary role in the present (pelagic) case as the natural convection effects are much smaller than the forced convection.

Tests with Larvae

Egg batches were obtained once a week from groups of adult northern anchovy maintained in the laboratory and induced to spawn. Measurements were made each week during a 6-wk period to minimize bias due to a single cohort group. Water temperature ranged from 19° to 21° C, and overhead fluorescent lighting was used. The 50% hatching point was determined and defined as "day 0" for each batch. Experiments were carried out on age day 0 larvae every week (six times).

A set of five 2,000 ml graduated cylinders filled with filtered seawater was used for the environmental tests. Oxygen concentrations of 100, 80, 60, 40, and 20% of saturation at the measured temperature were produced by bubbling nitrogen through each of the cylinders. After the larvae were added (about 25 individuals/cylinder), the cylinders were sealed off with rubber stoppers. Oxygen concentrations were measured periodically during the experiments with a Beckman Instrument Model 160 Physiological Gas Analyzer[2] to check on initial values and possible drift.

Individual fish were monitored for a 5-min period, and duration and number of swimming bursts were recorded on a Esterline-Angus Operation Recorder Model AW. Records were also made of approximate swimming direction (measured from horizontal) as well as the change in orientation of motionless larvae while they were sinking during the resting periods. Five active larvae were monitored in each container every week, for both day 0 and day 1 tests.

After the day 0 experiments were finished each week, the equipment was reset and the day 1 tests conducted 24 h later with additional larvae from the same batch. The latter larvae were kept in oxygen-saturated water from hatching to minimize stress due to oxygen starvation.

RESULTS

No appreciable change in the proportion of time spent in burst swimming was observed when the measurement at 100% of saturation concentration of oxygen (which is the oxygen level in the natural state in the sea because of turbulent interchange with the atmosphere) was compared with the time spent in motion at the 80 and 60% oxygen levels (Figure 3).

When oxygen levels were <60% of saturation, large increases in the time spent swimming were observed. The rate of increase of swimming time in both ages (day 0 and day 1) were similar. Various attempts at describing all five data points for each age-group by means of a single empirical exponential function were not successful (low coefficients of determination). Thus, it seems that a different behavioral mechanism is triggered when oxygen levels fall below 60% of saturation at the given temperatures, i.e., much lower than expected oxygen concentrations in the upper layers of the sea, where the anchovy larvae are usually found.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

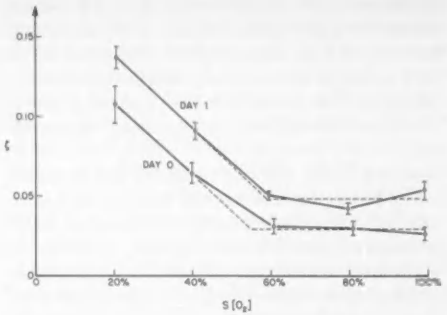

FIGURE 3.—Fraction of time spent actively swimming, ζ, versus oxygen concentration in percentage of saturation. S[O_2], for newly hatched (day 0) and 24-h-old (day 1) northern anchovy larvae. Each point on the full curves is an average of between 20 and 25 individual 5-min observations. Bounds are standard errors. Dashed lines indicate idealized model of constant fraction, ζ, at high S[O_2] and linearly increasing ζ at low S[O_2].

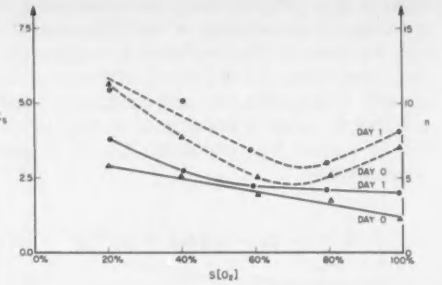

FIGURE 4.—Average duration (t) of swimming bouts (full lines) and number of bouts (n) in 5 min (dashed lines) for day 0 (solid triangles) and day 1 (solid circles) larvae, versus oxygen in percentage of saturation concentration (S[O_2]).

The duration of bursts increased monotonically as the oxygen levels decreased, while the number of bursts dropped significantly to a minimum of 1/min at 60-80%, increasing sharply after that (Figure 4). No satisfactory explanation has been found for the drop in the number of bursts at 80% of saturation. The main result illustrated by Figure 4 is that both the frequency and duration of bursts increase markedly at low oxygen concentrations, both contributing to the increase in time spent swimming.

The center of gravity of anchovy larvae is in the vicinity of the head and therefore they tend to be oriented in an oblique head-down configuration after swimming ceases. More mature larvae, which have converted significant amounts of yolk into denser tissue are negatively buoyant (Hunter and Sanchez 1976) and tend to sink head downward at rates of approximately 1-2 mm/s. To check the vertical station-keeping hypothesis, the direction of swimming was recorded, as well as the body orientation, when swimming started. The results of over 1,400 recorded swimming periods appear in Table 1, which lists average values of the body angle at the onset of swimming and the direction of swimming.

No significant variation in swimming direction with oxygen concentration was found for either day 0 or day 1 larvae (Table 1). The spread in results was large, as is noticeable from the standard errors. The total possible spread of data is $\pm 90°$, which suggests that swimming direction is actually a random phenomenon for day 0 larvae. At age 1 day, a positive bias was observed in the swimming direction, still with large variation. The body inclination at the beginning of the swimming periods was consistent, at around $-65°$ with the exception of the day 0, 20% oxygen data, which is influenced by additional factors, discussed below.

DISCUSSION

The analytical model predicted that a motionless larva would be able to pick up oxygen at a decreasing rate at any given spot (Equation 12).

TABLE 1.—Initial orientation of the body and duration of swimming during bouts of continuous swimming by newly hatched and 1-d-old northern anchovy larvae. Error bounds are standard error. Angles are measured from the horizontal. Positive values indicate upward motion. Averages of day 0 do not include 20% O_2 values as these (indicated by question marks) include different phenomena.

Oxygen concentration (% of saturation)	*N*, number of observed events		Orientation of body at start of swimming period (degrees)		Direction of swimming relative to horizontal (degrees)	
	Day 0 larvae	Day 1 larvae	Day 0 larvae	Day 1 larvae	Day 0 larvae	Day 1 larvae
100	106	157	−68.9±23.7	−74.6±11.8	−4.7±56.1	44.7±45.8
80	103	113	−66.3±29.4	−80.0± 9.2	−15.0±59.0	28.2±58.1
60	109	112	−72.1±15.6	−66.7±17.6	−3.9±73.6	51.9±31.9
40	161	140	−61.0±30.3	−69.2±22.0	12.3±54.0	33.2±45.9
20	210	204	−45.6±36.7(?)	−63.8±27.8	38.7±43.3(?)	37.4±52.3
Weighted average			−66.4±25.2	−70.2±16.9	−2.8±58.3	39.0±48.1

This prediction has now to be compared with the requirements of the organisms to determine if additional oxygen is needed. Data for oxygen consumption at 17° C of late-stage anchovy eggs and larvae of differing ages as a function of time since spawning has been obtained by Theilacker,[3] by measurement in a respirometer. These data were adjusted to 20° C, the temperature at which most of my experiments were conducted (Figure 5), by means of a temperature-growth correlation for larval northern anchovy (Zweifel and Hunter[4]). This adjustment was made by calculating the size of the larvae at 17° C at the ages recorded by Theilacker, then translating these into age for the same size at the new temperature, which gave a smaller size because growth rates increase with temperature. Thus, an estimate for the oxygen requirements at 20° C of size-defined larvae was obtained as a function of their age (the 20° C line in Figure 5).

The value of the ratio of oxygen consumption 1 d after hatching to that at hatching was about 1.6 (Figure 5). Returning now to Figure 3 we see that the ratio for the average percent of time spent swimming of the two age-groups is approximately 1.66. I conclude, therefore, that the distance between the day 0 and day 1 curves in Figure 3 is an indication of the increased general activity of the larvae as they grow. This correlation indicated in Figures 3 and 5 serves as an additional verification of both Theilacker's respirometer data and the present swimming data.

To compare experimental values of oxygen consumption to the prediction of the model we plot the data as Figure 6, where the horizontal lines show the range of oxygen requirements (from Theilacker's data) at hatching and 24 h later. The steady-state oxygen available by steady-state diffusion only (after the initial transient) obtained from the time-dependent first term in Equation (12) is now superimposed. Figure 6 indicates that pure diffusion supplies all the oxygen required for the day 0 larvae only when $<42\pm4\%$ of the O_2 saturation concentration is available. This changes to $63\pm4\%$ of saturation for the day 1 larvae. The sharp discontinuity in the swimming data, occurring be-

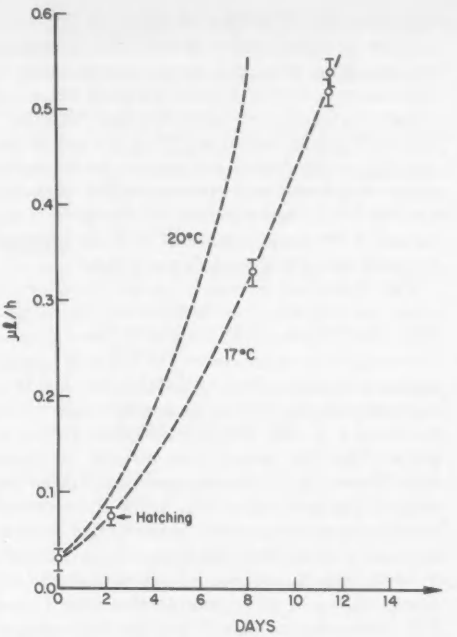

FIGURE 5.—Oxygen consumption by northern anchovy eggs and larvae versus time elapsed since spawning. Open circles indicate experimental data for 17° C. The line for 20° C is extrapolated from the 17° C data with the aid of the Zweifel and Hunter model (see text).

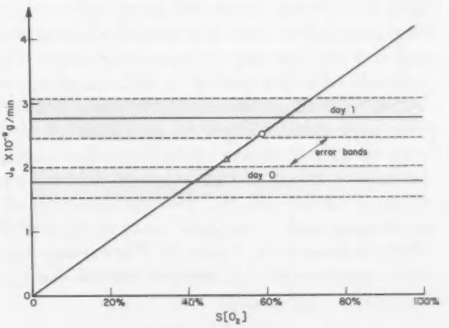

FIGURE 6.—Estimated oxygen requirements (J_o) of northern anchovy larvae at day 0 (hatching) and day 1, and steady-state oxygen supply by diffusion versus oxygen in percentage of saturation concentration ($S[O_2]$). The triangle and circle denote concentrations at which observed swimming behavior changes at day 0 and day 1, respectively (see Figure 3).

[3]G. Theilacker, Fishery Biologist, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92030, pers. commun. November 1978.

[4]Zweifel, J. R., and J. R. Hunter. 1978. Temperature specific equations for growth and development of anchovy (*Engraulis mordax*) during embryonic and larval stages. Unpubl. manuscr., 37 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

tween 60 and 40% oxygen concentration (Figure 3) can now be understood in terms of the theoretical results above. When the oxygen concentration in this water is 60% or higher, diffusion alone can satisfy the respiratory requirements of both day 0 and day 1 motionless larvae. Thus, the swimming activity at the higher concentrations is due to other factors, such as depth control. The measured activity level (Figure 3) does not change between 60 and 100% oxygen concentration, as expected from the theoretical model's predictions.

The increased swimming activity observed when the concentration drops below the 40-60% level must therefore be a respiratory reaction. Active swimming causes convective diffusion (which, as shown in the Analytical Model section, leads to much higher oxygen transport rates) and moves the larva to a new, nondepleted position. As expected from this mechanism, activity increases with decreasing ambient oxygen concentration, as oxygen transport rates drop below the required level faster at low ambient concentration, initiating motion more often. The dashed lines in Figure 3 verify this theoretical reasoning and the obtained values of 59% concentration (day 1) and 55% concentration (day 0) for the beginning of respiration-driven swimming are in very good agreement with Figure 6, especially considering the experimental errors involved in the various data sources.

Next, I consider the significance of swimming activity at higher oxygen concentration. The most plausible reason for the swimming behavior is to keep the larvae, which are negatively buoyant, from sinking out of the preferred depth zone in the sea. Day 1 larvae swim at an average angle of 39° upwards from the horizontal with no significant variation with oxygen concentration (Table 1). The large standard error is an indication of the wide spread of observed directions. The average swimming speed at this stage is 5.2±4.1 cm/s (Hunter 1972) and the average duration of a swimming bout (at oxygen concentration of 60-100%) is about 2.1 s (Figure 4). The average vertical component of the distance moved during a single bout is therefore

$$h_{up} = Vt \sin \alpha = 5.2 \cdot 2.1 \sin 39° = 6.9 \text{ cm}. \quad (16)$$

The uncertainty in this value is large due to the standard errors in both the swimming angle and the average swimming speed, but it is probably accurate at least to an order of magnitude. Between swimming periods, the larvae sink at a speed of 0.12±0.03 cm/s (Hunter and Sanchez 1976). The average number of swimming bouts per 5-min period was found to be about 7 (Figure 4), i.e., giving an average sinking time of 43 s. This leads to a vertical distance of 5.2 cm, which is close enough to the value of 6.9 cm of Equation (16) to show that the swimming of day 1 larvae at high oxygen levels most probably is a depth-control mechanism.

The newly hatched (day 0) larvae present a different situation. Pelagic eggs are slightly positively buoyant (Blaxter 1969) while the chorion, which is shed during hatching, is somewhat negatively buoyant. Thus, while no measurements independent of the present ones exist, it is reasonable to assume that these newly hatched larva are approximately neutrally buoyant due to their large yolk sac. As the yolk is consumed, the specific gravity increases and the sinking rates for day 1 are obtained. The larvae are approximately neutrally buoyant during the first hours after hatching so that no net sinking or upward swimming is expected. Table 1 shows that this is actually the case at day 0, where the average direction is very close to horizontal and the large error indicates almost random swimming direction. Some upward swimming may be discerned at the very low O_2 concentration experiments (20% O_2). This may be a result of an inadvertent oxygen gradient in the tank or a phototactic response induced by the low oxygen concentration. Phototaxis is probably the means by which the older larvae choose swimming direction, and is directed upwards as light in the present experiments comes from the surface.

ACKNOWLEDGMENTS

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DESCRIPTIONS OF LARVAL SILVER PERCH, *BAIRDIELLA CHRYSOURA*, BANDED DRUM, *LARIMUS FASCIATUS*, AND STAR DRUM, *STELLIFER LANCEOLATUS* (SCIAENIDAE)[1, 2]

HOWARD POWLES[3]

ABSTRACT

This paper presents descriptions and illustrations of larval *Bairdiella chrysoura* (3.1-8.8 mm standard length), *Larimus fasciatus* (3.0-5.9 mm standard length), and *Stellifer lanceolatus* (2.8-15.1 mm standard length). *Larimus fasciatus* larvae are characterized by brain pigment, pectoral fin pigment, and early-developing pectoral fin rays. Larval *B. chrysoura* resemble *S. lanceolatus*, but *B. chrysoura* have a swath of expanded melanophores from nape to cleithral symphysis. These two species also can be differentiated by the sequence of melanophores in the midventral line posterior to the anus. Off the southeastern United States, *L. fasciatus* spawn in continental shelf waters from May to October, and *B. chrysoura* and *S. lanceolatus* spawn in coastal and estuarine waters during late spring and summer.

The perciform family Sciaenidae is represented by 18 species off the southeastern United States (Table 1). Taxonomy of adult Sciaenidae of the western North Atlantic has recently been revised by Chao (1978); nomenclature in the present paper follows Chao (1978) rather than Bailey et al. (1970). Studies of larval sciaenids of the east coast of the United States have been numerous; these have recently been summarized in several publications (Scotton et al. 1973; Johnson 1978; Powles and Stender 1978; Lippson and Moran[4].) Despite the number of larval studies, their quality has been uneven; for example, larval series now known to consist of more than one species have been described as single species (*Menticirrhus americanus* and *Stellifer lanceolatus* of Hildebrand and Cable 1934), damaged or distorted specimens have been illustrated and described (*Sciaenops ocellata* of Pearson 1929; *Leiostomus xanthurus* of Hildebrand and Cable 1930), and illustrations have differed from descriptions of larvae of the same species in the same publication (early *Stellifer lanceolatus* of Hildebrand and Cable 1934). Further, few detailed developmental series of morphometric, meristic, and pigmentation data have been published, making separation of larvae to species impossible in the early stages before complete development of fin elements. Thus, both description of undescribed or incompletely described larvae and redescription of larvae which have been poorly described in the literature are necessary to specific identification of sciaenid larvae.

The three species whose larvae are treated in this paper are generally similar in habitat and probably in ecology. They are small fishes (maximum total lengths 20-23 cm) of coastal and estuarine waters (Hildebrand and Schroeder 1928; Hoese and Moore 1977). None are important commercial or sport fish, but all are abundant in estuaries (Dahlberg 1972; Shealy et al. 1974) and on coastal shrimp grounds (Anderson 1968; Keiser 1976). Because of their abundance and small size, all may be important prey items for larger, predacious fishes.

Descriptions of larvae of all three species have been published. Kuntz (1915) described eggs and yolk-sac larvae of *Bairdiella chrysoura* from eggs obtained from a ripe female and further described larvae and early juveniles from plankton collections. Since he examined live or fresh material rather than Formalin-preserved[5] material, it is to be expected that body proportions and pigment characters of his series might differ from those in

[1]South Carolina Marine Resources Center Contribution No. 94.

[2]MARMAP Contribution No. 164.

[3]Marine Resources Research Institute, Charleston, S.C.; present address: Gouvernement du Canada, Pêches et Océans, Division des Sciences halieutiques, C.P. 15500, Québec, Canada G1K 7Y7.

[4]Lippson, A. J., and R. L. Moran. 1974. Manual for identification of early developmental stages of fishes of the Potomac River estuary. Md. Dep. Nat. Resour., Power Plant Siting Program, PPSP-MP-13:1-282.

[5]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

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FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

larvae from preserved series. His description was cited by later authors (Hildebrand and Cable 1934; Scotton et al. 1973; Johnson 1978; Lippson and Moran see footnote 4) in compilations of larval

TABLE 1.—Reported meristics of South Atlantic Bight Sciaenidae. Counts in parentheses occur infrequently and semicolon indicates separate dorsal fins.

Species	Source[1]	Dorsal		Anal		Caudal procurrent	Vertebrae[2]	Gill rakers	
		Spines	Rays	Spines	Rays			Upper	Lower
Bairdiella chrysoura	1	X;I	19-23	II	8-10		12+13	7-8	14-16
	4	XI-XII	19-21	II	9-10				14-16
	5	XI;I	22	II	10			8	16
	7	XII	19-22	II	8-10	8-9, 5-8	11+14		
Cynoscion nebulosus	1	IX-X	25-28	II	10-11		(12)13+12(13)	2-3	7-9
	3		25		10-12		25		8
	4	X(XI);I	24-26	II	10-11				8
	5	X;I	25-27	II	10			4	7
	7	XI-XII	24-27	II	10-11		13+12		
	9		25-27		9-10	6-9, 5-7		4	6-8
C. nothus	1	X;I	26-30		8-10		15+12	3-4	8-10
	2		27-30(31)		8-9(10)		27(26)		12-14(15)
	3		24-28		8-10				12-14
	4	X;I	28-29	II	9				9
	5	X;I	27-29	II	9-10			4	9
	7	XI	28-30	II	9		14+13		
	9		26-29		9-11	7-8, 6-8			
C. regalis	1	X;I	26-29		11-13		(12)13+12(13)	4-5	10-13
	4	X;I	25-28	II	11-12				11-13
	5	X;I	26-29	II	11-13			5	11
	6	X-XI;I	24-29	II	10-12		14-15+10		
	7	XI	24-28	II	10-12	7-9, 5-7	13+12		
Equetus acuminatus	1	VIII-IX;I	37-41	II	7-8		10+15	5-6	9-14
	5	X;I	38-40	II	7			6	9
	7	X-XI	36-40	II	6-8		10+15		
	8	IX-X;I	37-40			7-8, 6-7			
E. lanceolatus	1	XII-XIII;I	47-55	II	6		10+15	5-6	10-13
	5	XIV-XVI;I	53	II	5			6	9
	7	XIII-XIV	46-50	II	6		10+15		
	8	XIII-XIV	49-55			7-8, 6-7			
E. punctatus	1	XI-XII;I	45-47	II	6-8		10+15	5	10-13
	5	XI-XII;I	46	II	6-7			6	11
	7	XIII	44-49	II	7-8		10+15		
	8	XI-XII;I	45-47			7, 5-7			
E. umbrosus	1	X-XI;I	38-40	II	7		10+15	4-6	10-12
	5	X;I	40	II	7				
	7	IX-XI	38-39	II	7	7-8, 7	10+15		
Larimus fasciatus	1	X;I	24-27				11+14	11-13	22-25
	4	X;I	24-27	II	6-8				23-25
	5	X;I	24-26	II	5-6			12	24
	7	XI-XII	25-27	II	6	6-7, 4-7	10+15		
Leiostomus xanthurus	1	IX;I	29-35	II	12-13		10+15	8-12	20-23
	4	X;I	30-34	II	12-13				22-23
	5	X;I	31	II	12			8	22
	7	XI-XII	29-32	II	12-13	6-8, 6-8	10+15		
Menticirrhus americanus	1	X;I	20-26	I	6-8		10+15	2-3	0-7
	4	X;I	24-27	I	7-8				6
	5	X;I	24-25	I	7				
	7	XI	24-26	II	7-8	8-9, 7	10+15		
M. littoralis	1	X-XI	19-26				10+15	3-5	0-8
	4	X;I	24-26	I	7				7-8
	5	X;I	23-25	I	7				7
	7	XI	24-25	II	7	7-8, 6	10+15		
M. saxatilis	1	X;I	22-27	I	7-9		10+15	3-5	0-7
	4	X;I	24-26	I	8-9				6
	5	X;I	26-27	I	8				
	7	XI	23-25	II	7-8	6-8, 6	10+15		
Micropogonias undulatus	1	X;I	27-30	II	8-9		10+15	8-10	14-18
	4	X;I	28-29	II	8				14-16
	5	X;I	28-29	II	7			7	16
	7	XI	28-29	II	8	8-9, 8	10+15		
Pogonias cromis	1	X;I	19-21	II	5-6		10+14	4-6	12-16
	4	X;I	20-22	II	6-7				14-16
	5	X;I	21	II	5-6			4	12
	7	XI	21-23	II	6	8-9, 7	10+14		
Sciaenops ocellata	1	X;I	23-25	II	8-9		10+15	4-5	7-9
	4	X;I	23-25	II	8				8-9
	5	X;I	24	II	8			5	7
	7	XI	23-25	II	7-8	8-10, 7-9	10+15		
Stellifer lanceolatus	1	XI-XII;I	20-24				11+14	10-13	22-23
	5	XI;I	20-23	II	7-8			13	22
	7	XII-XIII	21-24	II	7-9	7-9, 6-9	10+15		

TABLE 1.—Continued.

Species	Source[1]	Dorsal		Anal		Caudal procurrent	Vertebrae	Gill rakers	
		Spines	Rays	Spines	Rays			Upper	Lower
Umbrina coroides	1	X;I	26-31	II	6		11+14	5-7	7-10
	4	X;I	29	II	6				11
	5	X;I	27-28	II	6-7			5	9

[1]Sources:
1. Chao 1978
2. Ginsburg 1929
3. Hildebrand and Cable 1934
4. Hildebrand and Schroeder 1928
5. Jordan and Evermann 1896
6. Lippson and Moran (see text footnote 4)
7. Miller and Jorgensen 1973
8. Randall 1968
9. Welsh and Breder 1923.

[2]Includes urostyle.

sciaenids. Jannke[6] illustrated *B. chrysoura* of 2.0 and 5.0 mm SL (standard length). Hildebrand and Cable (1934) described a series identified as *Larimus fasciatus*. Although there is some disagreement between illustrations and descriptions of early larvae in this work, the series appears to represent a single species and to be correctly identified. Hildebrand and Cable also described larvae and juveniles identified as *Stellifer lanceolatus*. Their early larvae represent a mixed series; larvae <4 mm long had pectoral fin pigment and developed pectoral rays, but larvae >4.5 mm long had no pectoral pigment and pectoral rays that developed at ≥5.6 mm. Body proportions also changed between 4.0 and 4.5 mm. Their series appears coherent and correctly identified at lengths ≥5.6 mm. There were also some discrepancies between drawings and descriptions of early stages in their paper.

The purpose of the present paper is to redescribe larvae of these three species and to summarize characters for differentiating between the three species. In addition, notes are given on time and place of larval collections and on separation of larvae of these three species from those of other marine sciaenids of the southeastern United States.

METHODS

Approximately 50 specimens of each species were examined. Descriptions are based on the following numbers of specimens: silver perch, *Bairdiella chrysoura*, 21; banded drum, *Larimus fasciatus*, 21; star drum, *Stellifer lanceolatus*, 26.

Specimens on which descriptions were based were collected from continental shelf waters of the South Atlantic Bight, estuaries and tidal passes of South Carolina, and the Cape Fear River estuary of North Carolina. Those from continental shelf waters were collected with Boothbay neuston nets (mouth 1 m high × 2 m wide, mesh size 0.947 mm, tow velocity 2.6 m/s), MARMAP neuston nets (mouth 0.5 × 1.0 m, mesh size 0.505 mm, tow velocity 1.0 m/s), and 60 cm bongo nets (mesh size 0.505 mm, towing velocity 0.8 m/s) towed in a double oblique pattern between surface and bottom or 200 m depth. Specimens from South Carolina estuaries were collected with 0.5 m diameter conical nets (mesh size 0.571 mm, towing velocity 1.3-1.5 m/s) towed at surface or bottom. South Carolina tidal passes were sampled with 1.0 m mouth diameter plankton nets (mesh size 0.571 mm) moored to bridges or piers and fished near bottom for 1 h at early or middle flood tide. Specimens from the Cape Fear River estuary were collected with 1.0 m mouth diameter conical nets (mesh size 0.760 mm) towed at surface at 0.5 m/s. The number of samples available from each area except the Cape Fear River estuary by month (Table 2) provides an estimate of seasonal and areal effort distribution for comparison with data on time and place of capture of larvae. Tidal pass sampling was not carried out from August to January, and estuarine samples from August to December were not available. All specimens were preserved in 2% formaldehyde buffered by saturating with borax. Specimens from continen-

TABLE 2.—Numbers of plankton samples from South Carolina estuaries (1974), South Carolina tidal passes (1976), and the South Atlantic Bight continental shelf (1973-76) that were sorted for larval Sciaenidae.

Month	Estuaries		Tidal passes	Continental shelf	
	Surface	Bottom		Neuston	Bongo
Jan.	33	30	—	30	30
Feb.	17	14	2	30	30
Mar.	17	14	1	47	47
Apr.	33	28	1	52	38
May	19	17	2	48	48
June	17	17	5	—	—
July	16	16	8	—	—
Aug.	—	—	—	40	37
Sept.	—	—	—	39	1
Oct.	—	—	—	10	11
Nov.	—	—	—	31	16

[6]Jannke, T. E. 1971. Abundance of young sciaenid fishes in Everglades National Park, Fla., in relation to season and other variables. Univ. Miami Sea Grant Tech. Bull. 11:1-128.

tal shelf waters were initially fixed by immersing net cod ends in 8% formaldehyde for 2 min immediately following net washdown.

Measurements were made on the left side of the body, by ocular micrometer on a dissecting microscope. All measurements were made along or perpendicular to the body midline. Measurements are defined as follows:

Notochord length (NL) — symphysis of upper jaw to tip of notochord (measured in preflexion larvae).

Standard length (SL) — symphysis of upper jaw to posterior edge of hypurals (measured in larvae undergoing notochord flexion and in postflexion larvae).

Snout length — symphysis of upper jaw to anterior margin of eye.

Eye diameter — horizontal diameter of eye.

Head length — symphysis of upper jaw to posterior margin of opercular membrane.

Preanus length — symphysis of upper jaw to posterior margin of anus.

Snout to origin of spinous dorsal fin — symphysis of upper jaw to anterior margin of first developed dorsal spine base.

Snout to origin of soft dorsal fin — symphysis of upper jaw to anterior margin of first developed dorsal ray base.

Snout to dorsal fin termination — symphysis of upper jaw to posterior margin of last developed dorsal ray base.

Snout to anal fin origin — symphysis of upper jaw to anterior margin of first developed anal element base.

Snout to anal fin termination — symphysis of upper jaw to posterior margin of last developed anal ray base.

Anus to anal fin — posterior margin of anus to first developed anal element base.

Snout to pelvic fin insertion — symphysis of upper jaw to anterior margin of base of pelvic fin.

Depth at cleithral symphysis — vertical distance between dorsal margin of body and ventral symphysis of cleithra.

Depth at caudal peduncle — least vertical distance between dorsal and ventral margins of body in the area posterior to the terminal dorsal and anal fin rays and anterior to the hypural bones.

Fin counts include all elements of which any part (including pterygiophore) was developed. Counts were made in unstained specimens since the primary purpose of the study was to permit identification of specimens from field collections. Unless otherwise stated, lengths referred to in this paper are standard lengths.

Data on occurrences of larval *Larimus fasciatus* in plankton tows from continental shelf waters between Martha's Vineyard, Mass., and Palm Beach, Fla., were provided by Peter Berrien (Fisheries Biologist, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732). Collection methods and station distribution are given in Clark et al. (1969, 1970).

RESULTS

Bairdiella chrysoura

Morphology. Body proportions change gradually during larval development (Table 3). Body depth at the cleithral symphysis increases slightly with growth and is >30% SL in all specimens examined. Caudal peduncle depth remains constant through development. Preanus length increases from 40-45% SL in preflexion and flexion larvae to >50% SL at ≥5.7 mm. Positions of the dorsal, anal, and pelvic fins remain quite constant as the fins develop, whereas the decrease in length of the anus-anal fin gap corresponds to the increase in preanus length. Snout length and eye diameter change little during development, whereas head length increases from 27-31% NL or SL in preflexion and flexion larvae to 35% SL in larvae 4.9 mm.

Lateral and marginal preopercular spines are present throughout the series, becoming more numerous with growth until a maximum of five lateral and four marginal spines are present at 7.0-8.8 mm. A single posttemporal spine is present at 5.0-7.7 mm, and two such spines are present at 8.8 mm.

Fin development. The pectoral fin is present in all specimens examined; ray development begins at 5.7 mm and 16 rays are present by 8.8 mm (Table 4). Notochord flexion occurs at 4.1-4.4 mm SL. Development of caudal rays begins at the same time as notochord flexion. The full complement of principal rays is developed soon after completion of notochord flexion. Procurrent caudal rays begin to form at 5.7 mm and an incomplete procurrent ray count is present at 8.8 mm. The soft dorsal and anal fins begin ray development at the start of

TABLE 3.—Body proportions (percentage of NL or SL) of larval *Bairdiella chrysoura*. Specimens between dashed lines undergoing notochord flexion; lengths are NL above upper dashed line, SL below.

NL or SL (mm)	Snout length	Eye diameter	Head length	Preanus length	Snout to spinous dorsal origin	Snout to soft dorsal origin	Snout to soft dorsal termination	Anus to anal fin	Snout to anal fin origin	Snout to anal fin termination	Snout to pelvic fin insertion	Body depth at cleithrum	Caudal peduncle depth
3.1	8.7	10.0	30.0	42.5	–	–	–	–	–	–	–	35.0	–
3.5	6.8	10.3	31.0	41.3	–	–	–	–	–	–	–	31.0	–
3.6	7.4	9.8	27.6	40.4	–	–	–	–	–	–	–	30.8	–
3.7	7.4	10.6	30.8	41.4	–	–	–	–	–	–	–	31.9	–
3.7	6.3	10.5	27.3	40.0	–	–	–	–	–	–	–	32.1	–
3.8	7.4	9.5	28.7	44.6	–	–	–	–	–	–	–	32.9	–
4.1	7.2	11.7	31.5	46.8	–	54.1	77.5	15.4	62.2	74.8	–	35.1	8.1
4.4	10.6	12.4	37.2	48.7	42.5	61.9	83.2	17.7	66.4	81.4	–	37.2	9.7
4.4	8.9	11.1	30.3	44.6	40.1	57.1	76.7	21.7	66.3	80.3	–	33.9	7.1
4.8	9.8	11.4	31.1	45.9	39.3	57.3	78.6	16.3	62.2	73.7	–	33.6	6.5
4.9	7.9	10.3	37.3	48.4	38.9	57.1	82.5	16.7	65.1	80.2	35.7	36.5	10.3
5.0	8.6	10.9	35.2	49.2	39.9	57.8	83.6	17.9	67.1	80.5	35.9	36.7	10.1
5.7	8.6	11.4	35.7	48.6	38.6	60.0	82.9	17.1	65.7	80.0	35.7	37.1	11.4
5.7	8.6	11.4	35.7	51.4	37.1	58.6	82.8	11.4	62.8	81.4	37.1	37.1	11.4
7.0	7.0	11.6	37.2	57.0	37.2	59.3	82.5	8.1	65.1	80.2	38.4	37.2	11.6
7.5	10.9	10.9	35.8	55.4	38.1	59.8	81.5	7.6	63.0	78.3	35.8	35.8	10.9
7.5	8.7	10.9	36.9	53.3	39.1	57.6	83.7	11.9	65.2	79.3	35.8	35.8	8.7
7.7	10.6	10.6	38.3	58.5	43.6	59.6	82.9	9.6	68.1	80.8	40.4	37.2	10.6
8.8	9.3	11.2	36.4	56.1	39.3	59.8	85.0	8.4	64.5	79.5	39.3	36.4	10.3

TABLE 4.—Fin element counts of larval *Bairdiella chrysoura*. Specimens between dashed lines undergoing notochord flexion; lengths are NL above upper dashed line, SL below.

NL or SL (mm)	Spinous dorsal	Soft dorsal	Anal	Pectoral[1]	Pelvic	Caudal principal	Caudal procurrent
3.1	–	–	–	+	–	–	–
3.5	–	–	–	+	–	–	–
3.6	–	–	–	+	–	–	–
3.7	–	–	–	+	–	–	–
3.7	–	–	–	+	–	–	–
3.8	–	–	–	+	–	–	–
4.1	–	14	6	+	–	7+6	–
4.4	–	15	8	+	–	7+7	–
4.4	–	18	6	+	–	7+7	–
4.8	–	20	10	+	–	8+7	–
4.9	–	19	I,9	+	–	9+8	–
5.0	–	I,21	I,9	+	–	9+8	–
5.7	XI	21	II,9	+	3	9+8	3,1
5.7	XI	I,21	II,9	6	I,2	9+8	–
7.0	XI	I,21	II,9	11	I,5	9+8	4,3
7.5	XI	I,21	II,9	12	I,5	9+8	5,4
7.5	XI	I,22	II,9	8	I,5	9+8	4,4
7.7	XI	I,21	II,9	12	I,5	9+8	5,4
8.8	XI	I,22	II,9	16	I,5	9+8	6,5

[1] + = fin present, no developed elements.

notochord flexion and attain adult complements at ≥4.8 mm. The spinous dorsal begins development between 5.0 and 5.7 mm; spine development is rapid, with the adult complement present at 5.7 mm. Pelvic fins are first present at 5.7 mm and adult element complements are present at ≥7.0 mm.

Pigmentation. Larvae are characterized by an oblique swath of internal and external pigment, paralleling the cleithrum, from nape to cleithral symphysis (Figure 1). Melanophores of several areas constitute this swath: in the musculature of the nape, on the anterior and dorsal surfaces of the visceral mass, ventral to the brain, and on the ventral body surface. In small larvae (<5.0 mm), melanophores in these areas are usually expanded, so that a continuous swath of pigment is formed. Occasionally melanophores may be contracted, but are always present in the areas listed. In large larvae (≥5.0 mm), melanophores of these areas are more frequently contracted than in smaller larvae, and thickening of the body wall begins to obscure some of the swath pigment.

Pigment of the ventral midline of the tail begins as a continuous row of small melanophores in the smallest larvae and develops into a characteristic sequence of melanophores with growth. About 10 melanophores are present at 3.1-3.8 mm; one of these (two-thirds of the distance from anus to notochord tip) is larger than the others. In the dorsal midline of the tail, a few specimens ≤3.5 mm NL have a small melanophore dorsal to the large melanophore of the ventral midline. At ≥4.1 mm, melanophores of the ventral row are placed as follows: one or two anterior to the anal base, one at the origin of the anal fin, one at its termination, and three or four posterior to the anal fin. In most specimens ≥7.0 mm, no pigment is present anterior to the anal base, but the rest of the sequence remains, and small melanophores begin to appear at the bases of individual rays.

Other head and visceral mass pigmentation characterizes these larvae. A melanophore is present at the angle of the lower jaw throughout the series. Pigment is present at the tip of the

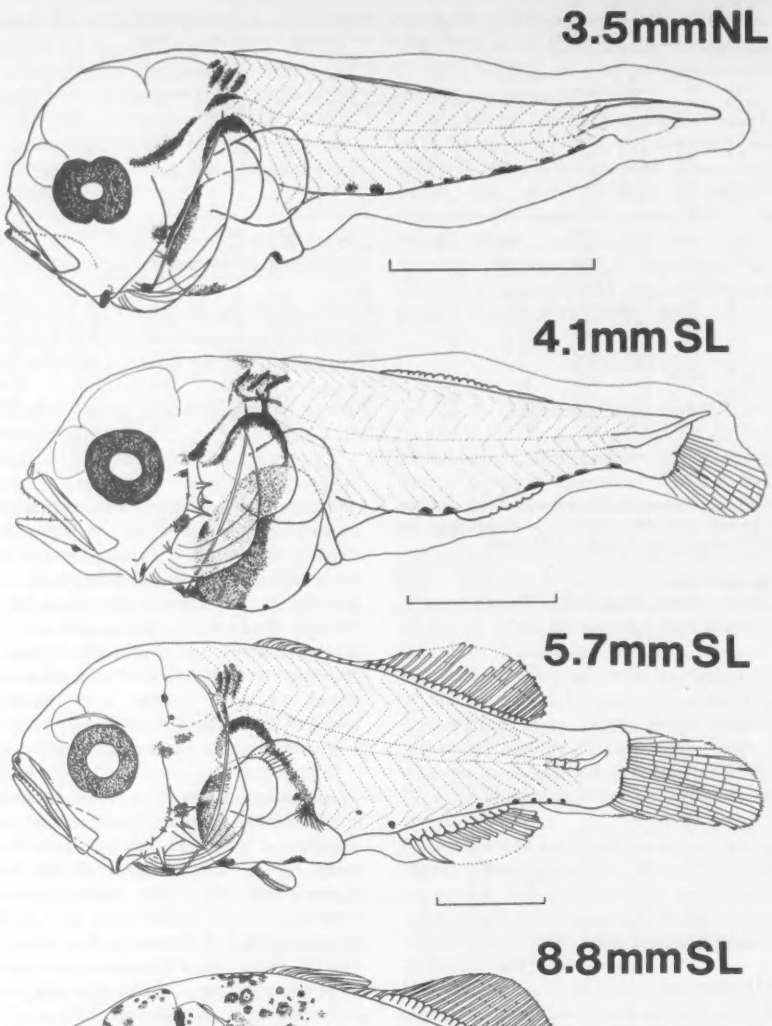

FIGURE 1.—Larval *Bairdiella chrysoura*. Scale equals 1 mm.

premaxillary at ≥5.7 mm and at the tip of the lower jaw at ≥7.5 mm. A melanophore is usually present on the medial surface of each dentary at 3.1-7.0 mm, while at ≥7.5 mm, one or several melanophores consistently occur in this position. Melanophores are present above the anterior part of the midbrain, and above the eye, at ≥7.0 mm. Melanophores are present on the surface of the midbrain at its junction with the hindbrain at ≥5.7 mm, and on the dorsal surface of the forebrain at ≥7.7 mm. Two melanophores occur in the midventral line on the ventral surface of the visceral mass: one midway between the cleithral symphysis and the anus (between the pelvic fin bases when these are developed), present at ≥3.3 mm, and another on the anterioventral surface of the anus, present at 3.1-5.0 mm. A melanophore midway between these is occasionally present at 3.5-4.7 mm and always present at ≥4.8 mm. On the posterior surface of the visceral mass, above the anus, a melanophore is present at ≥4.9 mm; this melanophore becomes increasingly branched and dark at ≥5.7 mm.

Body surface pigment increases in extent in late larvae (≥7.0 mm). This includes a cluster of melanophores in the dorsal midline anterior to the spinous dorsal fin, a group of melanophores ventral to this cluster, a group on the dorsal surface of the head, and a group on the lateral surface of the visceral mass.

Identification of the series. This series was identified as *B. chrysoura* by fin ray counts, pigmentation, caudal fin shape, and similarity to a published description. Fin ray counts (dorsal 21-22, anal 9) of late larvae in the series could have been attributed to *Menticirrhus americanus*, *M. saxatilis*, or *Stellifer lanceolatus* as well as *B. chrysoura*. A series of *Menticirrhus* larvae (identified by presence of a single mental barbel at ≥9.2 mm, tentatively as *M. americanus*), which I have examined, is characterized by heavy and extensive body pigment, and the absence of such pigment in larvae of the series described here indicated that it was *B. chrysoura* rather than *M. americanus*. Heavy body pigmentation has been described for *M. americanus* (Hildebrand and Cable 1934) and *M. saxatilis* (Scotton et al. 1973). Although species identifications in those descriptions may not be accurate, heavy body pigmentation is probably characteristic of larvae of the genus *Menticirrhus*. Caudal fin shape distinguished larvae of the series here described from larval *S. lanceolatus*. Late larvae of this series have the broadly rounded caudal fin characteristic of *B. chrysoura* (Hildebrand and Schroeder 1928; Dahlberg 1975) while late larvae of *S. lanceolatus* have the lanceolate caudal fin characteristic of the adult. Finally, larvae of my series are similar in major characters (the swath of pigment between head and visceral mass, midventral pigment posterior to the anus) to the larvae described by Kuntz (1915), which were apparently correctly identified.

Spawning season and area. Larval *B. chrysoura* occurred in six surface and six bottom tows in May and in five surface and five bottom tows in June 1974 in South Carolina estuaries. None occurred between January and April or in July. In South Carolina tidal passes, larvae occurred in two May samples, one June sample, and one July sample, and did not occur between February and April. A single specimen was taken in continental shelf waters, in a bongo net tow made in 31 m on 8 April 1974 (Figure 2). Thus spawning appears to occur primarily in coastal and estuarine waters of the southeastern United States, at least from April through July. Spawning may occur later in the year, but no samples after July from coastal and estuarine waters were examined.

Larimus fasciatus

Morphology. Body proportions change little during development (Table 5). The larvae are deep bodied (depth at cleithral symphysis >35% SL, except for a 3.8 mm specimen). Preanus length is >50% SL in all specimens but one. Positions of the fins change little during development. Anus to anal fin distance is variable in length, <6% SL in most larvae but with a maximum value of 10.2% SL. Caudal peduncle depth increases with development, from <9% SL at ≤4.2 mm to >9% SL in most larger specimens.

Preopercular spines are present in all larvae. Lateral spines are smaller than marginal spines, and numbers in both series increase with growth. One or two small posttemporal spines and a low, spinous supraorbital ridge are present at ≥5.5 mm.

Fin development. The pectoral fins are present throughout development (Table 6). Pectoral elements are first present at ≥4.0 mm; elements are incomplete at 5.9 mm, the largest larva available

TABLE 5.—Body proportions (percentage of NL or SL) of larval *Larimus fasciatus*. Specimens between dashed lines are undergoing notochord flexion. Lengths are NL above upper dashed line, SL below.

NL or SL (mm)	Snout length	Eye diameter	Head length	Preanus length	Snout to spinous dorsal origin	Snout to soft dorsal origin	Snout to soft dorsal termination	Anus to anal fin	Snout to anal fin origin	Snout to anal fin termination	Snout to pelvic fin insertion	Body depth at cleithrum	Caudal peduncle depth
3.0	10.4	10.4	33.8	53.2	–	50.6	68.8	–	–	–	–	50.6	6.5
3.2	9.6	12.0	36.1	53.0	–	–	–	–	–	–	–	39.8	7.2
3.6	10.9	13.0	35.9	55.4	41.3	53.3	76.1	4.4	59.8	71.7	39.1	39.1	8.7
3.8	9.2	12.2	34.7	49.0	–	–	–	10.2	59.2	70.4	–	33.7	6.1
4.0	10.8	12.8	38.8	56.8	–	52.0	76.8	4.0	60.8	74.4	35.6	39.6	9.2
4.2	7.3	11.9	36.7	54.1	36.7	50.5	81.7	5.5	59.6	71.6	37.6	37.6	8.3
4.3	10.1	13.8	40.4	57.8	39.4	55.0	81.7	5.5	63.3	74.3	35.8	40.4	9.2
4.3	8.2	12.7	38.2	57.3	41.8	54.5	85.5	3.6	60.9	71.8	39.1	40.9	8.2
4.4	9.7	13.3	38.1	58.4	43.4	58.4	89.4	8.9	67.3	75.2	36.3	42.5	10.6
4.5	9.6	13.2	36.8	54.4	40.4	49.1	86.0	9.6	64.0	76.3	36.0	37.7	8.8
4.8	8.1	13.8	41.5	65.0	41.5	58.5	87.0	4.1	69.1	78.9	40.7	41.5	10.6
4.9	10.3	14.3	37.3	61.9	40.5	57.1	87.3	0.8	62.7	77.0	39.7	44.4	10.3
5.0	9.4	15.0	40.2	58.3	39.4	55.1	87.4	4.7	63.0	75.6	39.4	46.5	11.0
5.5	7.5	13.4	35.8	59.7	41.8	56.7	89.6	4.5	64.2	77.6	37.3	44.8	11.9
5.7	10.3	14.5	37.9	60.0	38.6	57.9	89.0	5.5	65.5	79.3	37.2	44.1	11.0
5.8	9.9	12.7	38.0	60.6	42.3	59.2	87.3	1.6	62.0	74.6	39.4	45.1	11.3
5.9	12.5	13.9	40.3	59.7	44.4	59.7	87.5	5.6	65.3	76.4	37.5	43.1	9.7

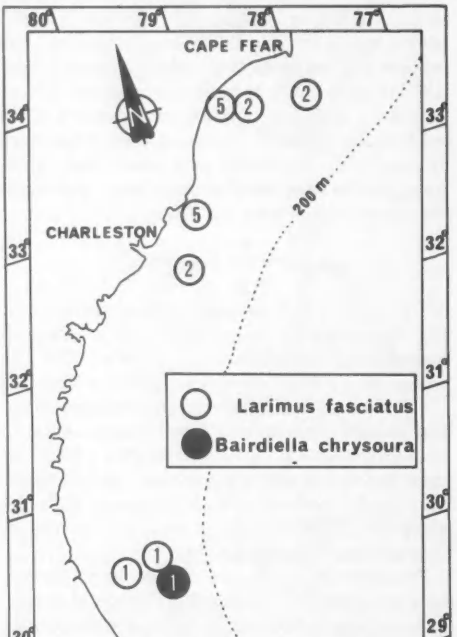

FIGURE 2.—Occurrence of larval *Bairdiella chrysoura* and *Larimus fasciatus* in South Carolina-MARMAP plankton tows in continental shelf waters of the South Atlantic Bight. Numbers indicate numbers of larvae at stations.

TABLE 6.—Fin element counts in larval *Larimus fasciatus*. Specimens between dashed lines are undergoing notochord flexion. Lengths are above upper dashed line, SL below.

NL or SL (mm)	Spinous dorsal	Soft dorsal	Anal	Pectoral[1]	Pelvic[1]	Caudal principal	Caudal procurrent
3.0	–	–	–	+	–	–	–
3.2	–	–	–	+	–	–	–
3.6	–	16	5	+	+	6+5	–
3.8	–	18	–	+	–	3+3	–
4.0	–	19	7	10	+	9+8	–
4.2	–	16	7	+	+	8+6	–
4.3	–	15	6	7	+	4+5	–
4.3	–	20	7	6	+	8+7	–
4.4	IX	27	II,6	11	I,4	9+8	–
4.5	III	22	7	10	+	8+6	–
4.8	X	25	6	10	+	9+7	–
4.9	X	27	II,6	12	I,3	9+8	–
5.0	X	26	II,6	10	I,1	9+8	–
5.5	X	27	II,6	15	I,5	9+8	0,1
5.7	X	27	II,6	14	I,4	9+8	0,1
5.8	XI	26	II,6	16	I,5	9+8	1,2
5.9	IX	27	II,6	15	I,5	9+8	2,2

[1] + = fin present, no developed elements.

(adult complement 17 in nine adults, 16 in one, all from South Carolina waters). Caudal flexion is occurring in specimens of 3.6-4.0 mm. Principal caudal rays are first seen in flexion specimens and are usually complete after 4.9 mm. Procurrent caudal rays appear at 5.5 mm and are incomplete in the largest specimen available. The soft dorsal fin base is present in the smallest larva, with no discernible elements; pterygiophores are countable at 3.6 mm and rays are consistently complete at ≥4.8 mm. Dorsal spines first appear at 4.4 mm

and are complete in one specimen at 5.8 mm. The anal fin is first present at 3.6 mm; the complete anal ray complement is present at ≥4.0 mm and anal spines are complete consistently at 4.9 mm. The pelvic fin bud is first present at 3.6 mm, and the complete element complement consistently present at ≥5.8 mm.

Pigmentation. Characteristic pigment patterns of the brain and pectoral fin are useful for identifying larval *L. fasciatus* (Figure 3). Melanophores are present on the anterior surface of the forebrain, the anterior and posterior surfaces of the midbrain, the posterodorsal surface of the hindbrain, and the ventral surface of the brain posterior to the eye, throughout the available series. The midbrain pigment appears to ring the midbrain when viewed from dorsally. The pectoral fin base and membrane are heavily pigmented throughout the series. Pigment in the membrane, diffuse in small larvae, is present between the rays when these are developed (≥4.3 mm). An expanded melanophore is present on the visceral mass just ventral to the pectoral fin base throughout the series; two or more melanophores may occur here at ≥4.2 mm.

Other head pigment includes two to four melanophores on the gular isthmus between the lower jaw rami, melanophores on the preoperculum posterior to the eye, a melanophore at the angle of the lower jaw, and one anterior to the cleithral symphysis.

In the ventral midline of the visceral mass, early larvae have three melanophores: one posterior to the cleithral symphysis (between pelvic fin bases when present), one midway between cleithral symphysis and anus, and one on the anteroventral surface of the anus. At ≥3.6 mm, the anus melanophore is absent, and at ≥4.5 mm, two or three melanophores may occur at the other two ventral midline locations. The anterior, dorsal, and posterior surfaces of the visceral mass are pigmented throughout the series, and at ≥5.0 mm, melanophores appear and increase in numbers on the lateral surface of the visceral mass.

In the ventral midline posterior to the anus, a row of six melanophores is present in the smallest larva (3.0 mm), the fifth of which, midway between the anus and notochord tip, is larger than the others. At ≥3.2 mm, two melanophores occur in the ventral midline, one at the position of the large melanophore of the original series (at the posterior end of the anal base when developed) and one anterior to this (just posterior to the anterior end of the anal base when developed).

In the dorsal midline, a melanophore is present anterior to the origin of the finfold or spinous dorsal at ≥3.8 mm; two or three melanophores may be present here at ≥4.5 mm. Two melanophores, one on either side of the midline, are present midway along the spinous dorsal base at ≥4.8 mm, and a similar pair of melanophores is present two-thirds of the distance along the soft dorsal base at ≥5.9 mm.

On the lateral surface of the body, between the spinous dorsal base and the visceral mass, melanophores appear at 4.4 mm and increase in number with growth.

Identification of the series. This larval series was identified as *L. fasciatus* by dorsal and anal fin ray counts, pigmentation, and by correspondence with a published description of late larval and early juvenile stages. Fin ray counts (dorsal 26-27, anal 6) observed in late larvae of this series could only have been of *L. fasciatus* or *M. americanus* (Table 1). The absence of heavy, extensive body pigmentation characteristic of *Menticirrhus* larvae indicated that the series described here was *L. fasciatus* rather than *M. americanus*. The pectoral fin pigment of the series here described is similar to that of *L. fasciatus* late larvae and early juveniles described by Hildebrand and Cable (1934). Although descriptions of early larvae in that paper are inadequate, late larvae (≥10.5 mm) and juveniles represent a coherent series apparently correctly identified.

Spawning season and area. No larval *L. fasciatus* were present in samples from South Carolina estuaries or tidal passes throughout the months sampled, January-July. In MARMAP tows in shelf waters, larvae were taken in April-May 1974, August-September 1974, and September 1975; larvae were most frequently taken on the inner two-thirds of the continental shelf and occurred from Cape Canaveral to Cape Fear (Figure 2). Information from plankton collections made by personnel of Northeast Fisheries Center Sandy Hook Laboratory (Figure 4) shows larval *L. fasciatus* to have been distributed across the width of the continental shelf and as far south as lat. 27°43′ N. Large collections of larvae (6-18 specimens) were common off northern Florida and southern Georgia. Larval *L. fasciatus* were taken in cruises made during May, July, and October off

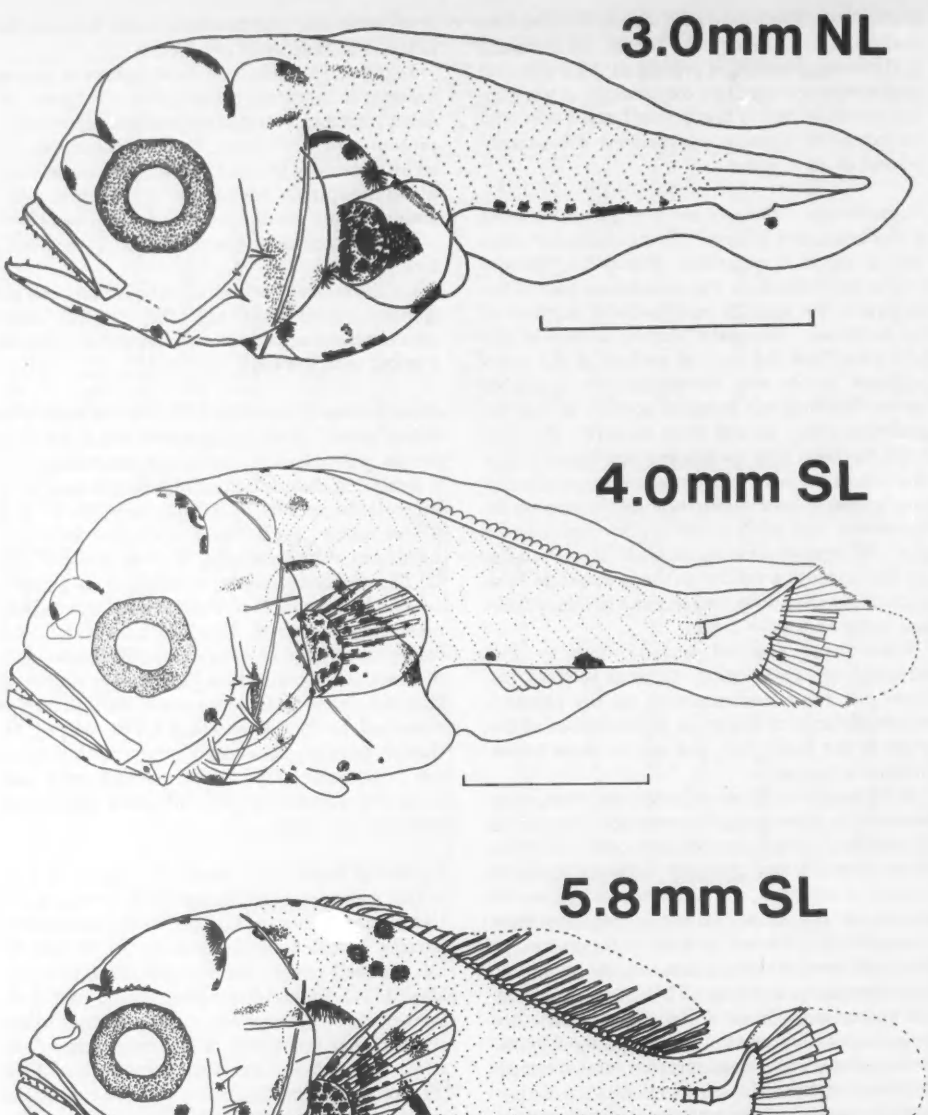

FIGURE 3.—Larval *Larimus fasciatus*. Scale equals 1 mm.

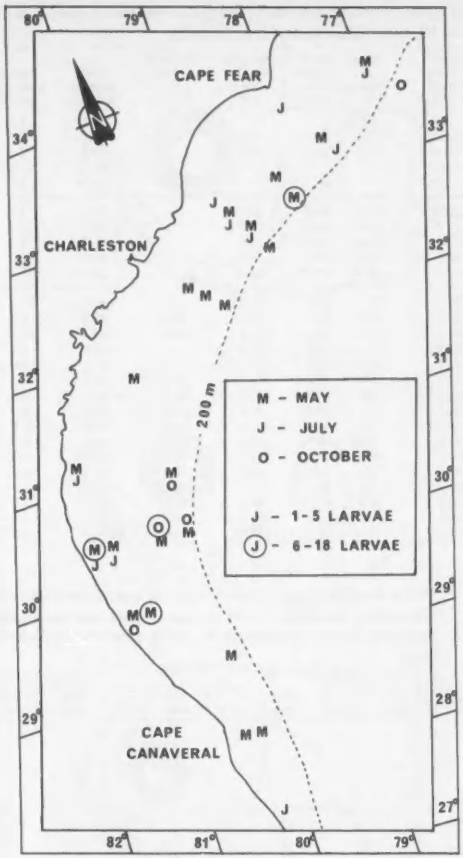

FIGURE 4.—Distribution of captures of larval *Larimus fasciatus* during plankton tows conducted by personnel of Northeast Fisheries Center Sandy Hook Laboratory off the southeastern United States (data supplied by Peter Berrien, Fishery Biologist, Northeast Fisheries Center Sandy Hook Laboratory, NMFS, NOAA, Highlands, NJ 07732).

the southeast United States; larvae were absent from the cruises made in January-February. On cruises made north of Cape Lookout, N.C., by Northeast Fisheries Center Sandy Hook Laboratory personnel, larval *L. fasciatus* were found as far north as lat. 36°22′ N (just south of the mouth of Chesapeake Bay); larvae were approximately as widely distributed and as abundant in continental shelf waters between Cape Lookout and Chesapeake Bay as off the southeastern United States (Berrien[7]). Larval *L. fasciatus* were collected in April to June and August to October on these "northern section" cruises.

Stellifer lanceolatus

Morphology. Body proportions change little during larval development (Table 7). The body is fairly deep (depth at cleithral symphysis 34-41% SL in most specimens). Preanus length, 40-50% SL through most of the series, increases to 55% SL in most late larvae (≥10.2 mm SL). Fins develop at the adult positions. The anus-anal fin gap, 12-20% SL in most specimens <8 mm, decreases with an increase in preanus length in larvae >10 mm. Head length increases slightly with development to the late larval stages; snout length and eye diameter change little over the size range available. Depth of the caudal peduncle increases slightly before and during notochord flexion and remains constant after flexion is complete.

Small lateral and large marginal preopercular spines are present throughout the series, as are premaxillary and dentary teeth. A posttemporal spine is present at 5.1-7.8 mm; at ≥10.2 mm a "scale bone" with four spinous projections is present in the posttemporal region.

Fin development. The pectoral fin, present throughout the series, first has elements at 6.9 mm and has the complete ray complement consistently at ≥14.0 mm, although the complete ray complement may be present in smaller larvae (Table 8). Notochord flexion occurs between 3.3 and 4.3 mm. Principal caudal rays are present in one preflexion larva and are consistently present during and after flexion; the adult complement is present at ≥5.5 mm. Procurrent caudal rays first appear at 5.1 mm and are complete at ≥10.2 mm. Bases of the soft dorsal and anal fins are present, with no discernible elements, in two preflexion specimens, and are consistently present with developed pterygiophores in flexion and postflexion specimens. Complete anal ray counts occur at ≥3.3 mm, and complete anal spine complements at ≥5.5 mm. Dorsal ray complements are consistently complete at ≥5.5 mm although complete counts may occur at 4.5 mm. Dorsal spines are occasionally seen at 4.5-5.8 mm and are consis-

[7]Peter L. Berrien, Fishery Biologist, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun. June 1979.

TABLE 7.—Body proportions (percentage of NL or SL) of larval and juvenile *Stellifer lanceolatus*. Specimens between dashed lines are undergoing notochord flexion. Lengths are NL above upper dashed line, SL below.

NL or SL (mm)	Snout length	Eye diameter	Head length	Preanus length	Snout to spinous dorsal origin	Snout to soft dorsal origin	Snout to soft dorsal termination	Anus to anal fin	Snout to anal fin origin	Snout to anal fin termination	Snout to pelvic fin insertion	Body depth at cleithrum	Caudal peduncle depth
2.8	8.2	11.0	30.1	45.2	–	–	–	–	–	–	–	37.0	6.8
2.9	9.3	10.7	33.3	45.3	–	50.6	66.7	13.3	58.6	69.3	–	37.3	6.7
3.1	8.8	11.4	32.9	41.7	–	48.0	69.6	21.5	63.2	74.6	–	38.0	7.6
3.1	8.9	11.4	35.4	41.8	–	–	–	–	–	–	–	35.4	7.6
3.5	6.6	11.0	27.4	39.5	–	–	–	–	–	–	–	34.1	6.6
3.3	5.9	12.9	34.1	47.1	–	61.2	90.5	18.7	65.8	84.7	–	41.2	9.4
3.4	6.9	11.5	36.8	46.0	–	51.7	77.0	13.6	59.8	74.7	–	40.3	8.1
3.8	7.2	9.3	27.8	41.2	–	49.4	70.1	17.6	58.8	73.2	–	35.0	6.2
4.1	7.5	11.3	31.1	45.3	39.6	54.7	86.8	15.1	60.4	79.2	–	39.6	10.4
4.3	8.2	11.8	31.8	45.5	–	53.6	81.8	16.3	61.8	78.2	–	38.2	10.9
4.5	8.7	11.3	34.7	48.7	35.7	57.4	86.1	12.1	60.8	77.3	37.4	40.8	11.3
4.9	8.7	9.5	32.5	42.9	36.5	55.6	83.3	19.0	61.9	80.2	30.2	36.5	8.7
5.1	9.7	12.9	35.5	48.4	35.5	56.4	87.1	12.9	61.3	77.4	35.5	38.7	9.7
5.5	7.5	10.4	32.8	43.3	32.8	49.3	80.6	14.9	58.2	76.1	–	35.8	9.0
5.5	9.0	10.4	31.3	47.8	34.3	52.2	90.0	11.9	59.7	79.1	–	37.3	9.0
5.8	7.0	14.1	31.0	43.7	35.2	50.7	84.5	15.5	59.2	76.1	32.4	32.4	8.5
6.2	8.0	8.0	32.0	46.7	34.7	54.7	82.7	12.0	58.7	76.0	32.0	36.0	9.3
6.9	8.3	9.5	34.5	45.2	36.9	54.7	82.1	14.3	59.5	76.2	29.7	33.3	9.5
7.4	10.0	10.0	37.8	54.4	41.1	56.7	84.4	8.9	63.3	77.8	41.1	37.8	10.0
7.6	8.6	8.6	35.4	47.3	37.6	55.9	86.0	11.8	59.1	76.3	31.1	34.4	9.7
7.8	7.4	9.5	32.6	45.3	35.8	53.6	83.2	12.6	57.9	79.0	30.5	35.8	9.5
10.2	8.8	9.6	38.4	55.2	40.0	59.2	85.6	8.8	64.0	79.2	38.4	36.0	5.6
13.1	10.3	9.0	38.5	57.6	38.5	58.9	85.9	6.5	64.1	78.2	39.7	35.8	9.0
13.9	9.6	7.2	39.7	54.2	38.5	59.0	85.5	9.7	63.9	78.3	36.1	33.7	9.6
14.0	9.0	8.0	37.3	55.4	36.2	54.1	85.5	8.4	63.8	78.3	38.5	33.7	9.8
15.1	10.0	8.9	38.9	57.8	36.7	55.5	84.5	7.7	65.5	77.7	38.9	33.3	8.9

tently present at 6.2 mm; the adult complement is consistently present at ≥10.2 mm. The pelvic fin bud is first present at 4.9 mm and is consistently present at ≥6.2 mm; adult element complements are present at ≥6.9 mm.

Pigmentation. Pigmentation of the body posterior to the anus is of particular value in identification of larval *S. lanceolatus* (Figure 5). In the ventral midline, small larvae (≤3.1 mm) have a row of five or six melanophores between the anus and the notochord tip; one or two of these, two-thirds of the distance from anus to notochord tip, are larger than the others. In larger specimens, an expanded melanophore is present two-thirds of the distance from anus to notochord tip (at the posterior end of the anal base when developed); this melanophore branches dorsally, often as far as the midlateral line. In some specimens (as shown, Figure 5) two expanded, branching melanophores are present at the posterior end of the anal fin base. In most specimens ≥3.1 mm, a melanophore is present (at the anterior end of the anal base when developed) anterior to this expanded melanophore. One to three small melanophores are present posterior to the anal base in most specimens 3.3-6.2 mm; none are present at 6.9-10.2 mm, and at >10.2 mm three or four melanophores are present here. A small, faint pigment spot is present in the midlateral line above the melanophore at the posterior end of the anal base in some specimens 3.1-5.5 mm, often connected to

TABLE 8.—Fin element counts in larval and juvenile *Stellifer lanceolatus*. Specimens between dashed lines are undergoing notochord flexion. Lengths are NL above upper dashed line, SL below.

NL or SL (mm)	Spinous dorsal	Soft dorsal	Anal	Pectoral[1]	Pelvic[1]	Caudal principal	Caudal procurrent
2.8	–	–	–	+	–	–	–
2.9	–	–	–	+	–	–	–
3.1	–	–	–	+	–	–	–
3.1	–	–	–	+	–	2+2	–
3.5	–	–	–	+	–	–	–
3.3	–	15	8	+	–	6+6	–
3.4	–	19	7	+	–	4+5	–
3.8	–	18	8	+	–	8+7	–
4.1	–	17	I,8	+	–	8+7	–
4.3	–	19	8	+	–	8+6	–
4.5	II	21	II,8	+	–	9+8	–
4.9	–	20	I,8	+	+	9+7	–
5.1	V	19	II,8	+	–	9+8	1,1
5.5	–	19	I,8	+	–	8+7	–
5.5	–	22	II,9	+	–	9+8	1,1
5.8	–	22	II,8	+	–	9+8	–
6.2	VII	22	II,8	+	+	9+8	2,2
6.9	XI	I,22	II,8	7	I,4	9+8	4,3
7.4	XI	I,23	II,8	13	I,5	9+8	4,4
7.6	XI	I,22	II,8	7	I,3	9+8	5,4
7.8	XI	22	II,8	13	I,5	9+8	6,4
10.2	XI	I,23	II,8	19	I,5	9+8	3,8
13.1	XI	I,22	II,8	19	I,5	9+8	9,8
13.9	XI	I,22	II,8	15	I,5	9+8	9,8
14.0	XI	I,23	II,8	19	I,5	9+8	9,8
15.1	XI	I,21	II,8	20	I,5	9+8	9,8

[1] + = fin present, no developed elements.

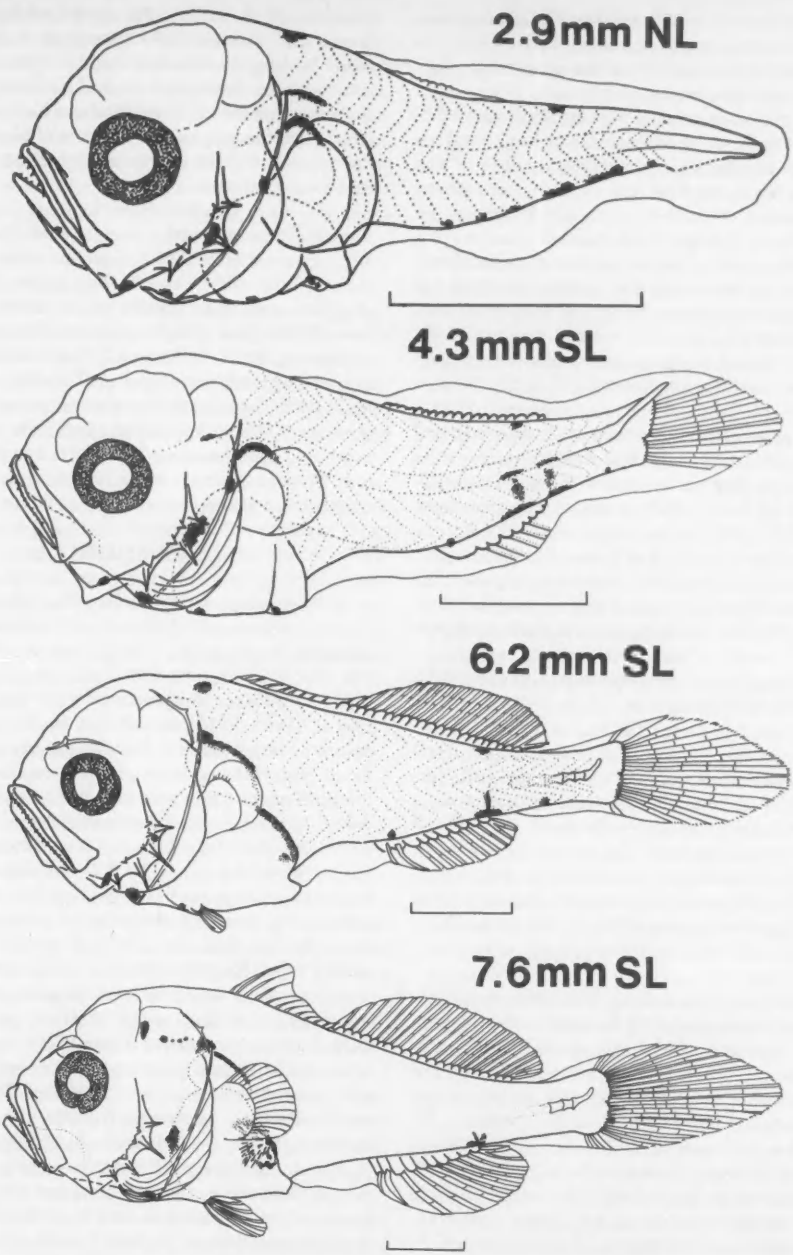

FIGURE 5.—Larval *Stellifer lanceolatus*. Scale equals 1 mm.

the dorsal branches of the expanded melanophore. A melanophore is present in the dorsal midline dorsal to the melanophore at the anal fin termination in most specimens 2.9-6.2 mm.

Head and visceral mass pigment is also useful in identifying larval *S. lanceolatus*. A large melanophore is present on the anterior surface of the visceral mass, between the cleithra, throughout development. A similar melanophore appears on the posterior surface of the visceral mass at ≥4.1 mm; this melanophore becomes extensively branched at ≥6.9 mm, and additional expanded melanophores appear dorsal and ventral to this one at ≥10.2 mm. In the ventral midline of the visceral mass a melanophore is present midway from cleithral symphysis to anus at 2.9-6.2 mm (between pelvic fin bases when present), and a second melanophore occurs on the anteroventral surface of the anus at 2.9-5.8 mm. In small larvae (≤3.8 mm), pigment is present in the dorsal midline and internally, on both sides of the notochord, above the visceral mass. A characteristic pigment area at the dorsal end of the operculum, which appears to roof a cavity in this area, is present at ≥7.4 mm. Pigment occurs at the angle of the lower jaw at <6.2 mm and anterior to the cleithral symphysis throughout the development.

Further pigment develops in late larvae (>10.2 mm). On the body surface, this includes a scattering of melanophores between the spinous dorsal and the visceral mass, four clusters of small melanophores in the dorsal midline along the dorsal fin base, and a few internal melanophores in the midlateral line above the anal base. Small melanophores appear in the spinous dorsal membrane and at the tip of the caudal fin at 13.1 mm, and in the soft dorsal membrane at 15.1 mm. Even in late larvae, pigmentation is not particularly heavy.

Identification of the series. The series was identified as *S. lanceolatus* by fin ray counts, pigmentation, caudal fin shape, and similarity to a published description of late larvae and juveniles. Fin ray counts of late larvae in this series (dorsal 21-23, anal 8) could be those of *B. chrysoura, M. americanus, M. saxatilis,* or *S. lanceolatus* (Table 1). Lack of heavy extensive body pigment indicates that the series is not *Menticirrhus*. The late larvae of the series have a lanceolate caudal fin, characteristic of *S. lanceolatus* but not of *B. chrysoura* (Hildebrand and Schroeder 1928; Dalhlberg 1975). Late larvae (≥9 mm) and early juveniles of *S. lanceolatus* described by Hildebrand and Cable (1934) represent a coherent series leading to a correctly identified young adult; late larvae of the series described here are similar to the late larvae of Hildebrand and Cable (1934), notably in the presence of an area of pigment at the upper end of the operculum, which appears to roof a cavity in this area.

Spawning season and area. Larval *S. lanceolatus* occurred in two South Carolina estuary samples in June and in one in July 1974; all three samples came from bottom rather than surface tows. Tidal pass sampling yielded five samples containing larvae in June and five with larvae in July; no larvae were taken from February to May. No *S. lanceolatus* larvae were taken in continental shelf tows. Thus, spawning appears to occur in estuarine and coastal waters, and not in shelf waters. Spawning occurs in early summer and may continue later into the year.

DISCUSSION

Comparisons with earlier descriptions

Bairdiella chrysoura

My material is in agreement with the description of Kuntz (1915), except that fin development occurs at larger sizes in Kuntz's description than in my material, and some pigment details are different. Kuntz's 5 mm specimen had a flexing notochord, 13 caudal rays, a developing dorsal fin base, and no anal base; these characters are found in my larvae of 4.3-4.4 mm. His 7.5 mm specimen is equivalent to my specimens of about 5.0 mm, having about 25 dorsal fin elements, 11 anal elements, no pelvic fin buds, and the full complement of caudal rays. Kuntz's larvae of ≤7.5 mm had a melanophore in the dorsal midline above the large melanophore of the ventral midline, present in only a few specimens ≤3.5 mm SL in my series, and a melanophore anterior to the dorsal fin origin, present in none of my specimens. These discrepancies may be due to Kuntz's use of fresh material while I used formaldehyde-preserved material. Shrinkage of formaldehyde-preserved larvae could account for the developmental differences, and melanophores may be contracted during preservation or degraded with storage in formaldehyde. Kuntz probably used total lengths rather than standard lengths which might par-

tially account for development rate discrepancies.

Jannke (see footnote 6) illustrated 2.0 mm and 5.0 mm larvae identified as *B. chrysoura*. The 2.0 mm specimen, smaller than my smallest larva, does not resemble Kuntz's larvae at similar sizes nor my earliest specimen in pigmentation. Jannke's 5.0 mm specimen is probably correctly identified: it has the fin counts and the characteristic cleithral pigment swath of *B. chrysoura* but lacks characteristic pigment of the ventral midline.

Larimus fasciatus

My material agrees fairly well with the only published description, that of Hildebrand and Cable (1934). The pigmented pectoral fin, emphasized by Hildebrand and Cable (1934), would appear to confirm identification of all specimens of their series. The drawings are not in good agreement with the description in their text; for example, their drawing of a 4.5 mm specimen shows none of the pigment described. The pigment of the brain which I have found characteristic of *L. fasciatus* larvae was not mentioned by Hildebrand and Cable; perhaps fading due to preservation was responsible. The few body proportions given by Hildebrand and Cable (particularly the position of the anus at >50% SL) are characteristic of *L. fasciatus*.

Stellifer lanceolatus

Hildebrand and Cable's (1934) description of a series identified as *S. lanceolatus* was based on a mixture of that species and *L. fasciatus*. Early larvae (≤3.5 mm SL) had pigmented pectoral fins and developing pectoral rays characteristic of *L. fasciatus*. Later larvae (≥4.5 mm SL) lacked pectoral fin and brain pigment and showed pectoral ray development only at >5.6 mm. Body depth and preanus length values of the early larvae are closer to those of *L. fasciatus* than of *S. lanceolatus*. Characters given by Hildebrand and Cable (1934) for separating early *L. fasciatus* and *S. lanceolatus* were preopercular spination, mouth shape, maxillary length, and amount of space around the brain. However, my observations indicate that none of these characteristics are suitable for separating these species.

As with *L. fasciatus*, there are discrepancies between text and illustrations in the description of Hildebrand and Cable (1934), particularly in the early stages. My material agrees fairly well with that of Hildebrand and Cable (1934) at ≥4.5 mm SL, although I observed a dorsal midline melanophore dorsal to the termination of the anal fin in specimens ≤7.0 mm SL, which was not indicated by those authors.

Spawning Seasons and Areas

Bairdiella chrysoura

Spawning is reported by various authors to occur in late spring and summer on the east coast of the United States and the Gulf of Mexico, and year-round in South Florida. The season appears to begin later and to be shorter at higher latitudes: June to August off New Jersey (Welsh and Breder 1923), May to July in Delaware Bay (Thomas 1971) and Chesapeake Bay (Hildebrand and Schroeder 1928; Joseph et al. 1964), April to August at Beaufort, N.C. (Kuntz 1915), April to May off Georgia (Dahlberg 1972), and April to September off Louisiana (Sabins 1973). Year-round spawning with peaks in January to February and April to June is reported in South Florida (Jannke see footnote 6). Spawning occurs at least April to July in South Carolina waters, according to data presented in the present study.

Spawning reportedly occurs primarily in estuarine and coastal waters, and this is indicated by my data also. Hildebrand and Cable (1930) reported captures of eggs and early larvae in estuaries and to 19-24 km offshore off Beaufort, N.C., but the reliability of their identifications is uncertain. Their descriptions of eggs and early larvae of *B. chrysoura* are insufficiently detailed to ensure separation from those of other sciaenid and perciform fishes. Jannke (see footnote 6) and Sabins (1973) judged from the small size of larvae caught in tidal passes that spawning must have occurred nearby in estuarine or coastal waters. Specimens I examined were mostly taken in South Carolina estuaries and tidal passes, with only one specimen coming from continental shelf waters.

Larimus fasciatus

The information I have presented and the limited literature reports available indicate a long spawning period, extending at least from May to October, for *L. fasciatus*. Although larvae were more abundant in MARMAP tows made from August to September than tows made from April to May, larvae were abundant in NMFS Sandy Hook

Laboratory plankton tows made in May and in July. Hildebrand and Cable (1934) took specimens of length <5 mm from July to October off Beaufort, but presence of small juveniles in these months indicated spawning began in May. Larvae were taken from April to October in plankton tows between Chesapeake Bay and Cape Lookout, N.C. (Berrien et al. 1978).

Spawning apparently occurs in continental shelf waters. I obtained no larvae from South Carolina estuaries, but larvae were abundant in continental shelf plankton tows. Hildebrand and Cable (1934) took larvae from the coast to 22 km offshore. Larvae were common in plankton tows in continental shelf waters between Chesapeake Bay and Cape Lookout (Berrien et al. 1978).

Stellifer lanceolatus

My data point to spawning at least in June and July in South Carolina waters; later spawning may occur but no samples were available from the second half of the year. Hildebrand and Cable (1934) reported presence of small larvae from July to September, but their small "*S. lanceolatus*" were probably *L. fasciatus* so this report may not be accurate. Welsh and Breder (1923) reported spawning in late spring and early summer on the U.S. east coast, and Dahlberg (1972) reported May to September spawning off Georgia. Fahay (1975) reported a 28.2 mm SL specimen taken in October off Florida.

Spawning in coastal and estuarine waters rather than continental shelf waters was indicated by my observations. Hildebrand and Cable (1934) reported small larvae from the coast to 22 km offshore, but again these larvae may have been misidentified. Larvae have been taken in Georgia estuaries (Berrien[8]). Fahay's (1975) single specimen was from inshore 7.5 km south of Cape Canaveral; being relatively large, this specimen could have originated in another spawning area.

Comparisons With Other Larval Sciaenidae

Larimus fasciatus

Although superficially similar to larvae of several other marine sciaenids, of the southeast United States, *L. fasciatus* larvae are easily separated from all others by pigmentation, fin development sequence, and preanus distance. Forebrain pigment and pectoral fin pigment are not present in early larvae (larvae with dorsal and anal fin rays undeveloped or incompletely developed) of other sciaenids of the area, and pigment on the anterior surface of the midbrain appears earlier than in other sciaenids of the area. Pectoral fin rays begin development earlier than in other sciaenids of the area, in fact earlier than in larvae of most known teleosts. The preanus distance of >50% SL is greater than in other sciaenid larvae of the area.

Bairdiella chrysoura and *Stellifer lanceolatus*

These species are treated together because they are quite similar as larvae, and resemble larvae of other species, notably *Cynoscion regalis* (Pearson 1941) and *Cynoscion nothus* (Stender[9]). Typical larvae of *B. chrysoura* have a well-developed swath of pigment from nape to cleithral symphysis, which is not found in larvae of the other species; however, melanophores of the swath may be contracted or faded by preservation. Pigment of the ventral midline posterior to the anus is the most reliable character for separation of *B. chrysoura* from *S. lanceolatus* larvae. Both have a melanophore at the posterior end of the anal fin base; however, *B. chrysoura* has a melanophore anterior to the anal fin base (at 4.1-7.0 mm SL) and a melanophore at the anterior end of the anal base, while *S. lanceolatus* has no melanophore anterior to the anal base but has a melanophore just posterior to the anterior end of the anal base (at the base of the second anal spine when this is developed).

Larvae of the two *Cynoscion* species mentioned can be separated from larval *B. chrysoura* and *S. lanceolatus* by careful attention to pigment of the midventral line (Stender see footnote 9; pers. observ.). Identification of small larvae with undeveloped anal fin bases may be difficult, since the characteristic pigment sequences develop (from a row of small melanophores) at about the same time as anal-base development. Presence of a melanophore in the dorsal midline, above the posterior end of the anal base, in most *S. lan-*

[8]Peter L. Berrien, Fishery Biologist, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun. May 1975.

[9]Bruce W. Stender, Biologist, South Carolina Wildlife and Marine Resource Division, P.O. Box 12559, Charleston, SC 29412, pers. commun. February 1978.

ceolatus 2.9-6.9 mm SL may also assist in separating the species; such a melanophore is present in only a few *B. chrysoura* at ≤3.5 mm SL.

Cynoscion regalis has a single melanophore in the dorsal midline above the anal fin throughout development.

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REPRODUCTIVE BIOLOGY OF THE VERMILION SNAPPER, *RHOMBOPLITES AURORUBENS*, FROM NORTH CAROLINA AND SOUTH CAROLINA

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ABSTRACT

The vermilion snapper, *Rhomboplites aurorubens*, a species often associated with Caribbean reefs and banks, is an important recreational fish of the outer continental shelf of North Carolina and South Carolina. Serial spawning occurs from late April through September off the Carolinas at depths ranging from 31 to 91 m. Most females spawn in the third or fourth year at about 205-275 mm total length. Larger, older females (age 5-10; up to 530 mm total length) appear to spawn longer each reproductive season, which may be an optimal strategy for maximizing reproductive biomass (balancing the physiological costs of somatic and gonadal growth).

Overall sex ratio is unequal in favor of females (approximately 60%), but the ratio is 1:1 for small fish (less than 150 mm total length) and heavily in favor of large females (69-100% for fish greater than 500 mm total length) because they live longer than males. Fecundity of first spawners is estimated at 17-42 thousand eggs, and large females produce 1.5 million eggs.

The vermilion snapper, *Rhomboplites aurorubens*, is a small lutjanid which grows to 600 mm total length (TL) and 2,600 g (illustrated in Böhlke and Chaplin 1968). It occurs from Cape Hatteras, N.C., to Bermuda, southward throughout the Gulf of Mexico and Caribbean Sea to southeastern Brazil. The species is abundant, ranking second or third in weight and numbers in the Carolina headboat[3] fishery (which landed between 590 and 730 metric tons of demersal fishes annually) between 1972 and 1975 (Huntsman 1976).

Vermilion snapper and other reef fishes normally associated with deep (>70-90 m) Caribbean reefs and banks occur in two habitats of the outer continental shelf of the Carolinas (Figure 1). The most spectacular of the habitats, the shelf break zone (Struhsaker 1969), occurs at the edge of the continental shelf (55-180 m) where the gently sloping bottom plunges abruptly downward as the continental slope. It is an area of jagged peaks, precipitous cliffs and rocky ledges associated with drowned Pleistocene reefs (MacIntyre and Milliman 1970). The second habitat (inshore live bottom) occurs at 25-55 m and consists of broken reefs and rock outcroppings, rocky ledges, and coral patches dispersed over the continental shelf shoreward of the shelf break zone.

Knowledge concerning reproduction of the vermilion snapper is lacking. Longley and Hildebrand (1941) reported gravid specimens about the Tortugas, Fla., in July and concluded that spawning takes place in midsummer. Breder (1929) wrote that vermilion snapper probably spawn in early spring along the South Atlantic coast of the United States, and Walker (1950) reported spawning off North Carolina in February. Monroe et al. (1973) collected a ripe female off Jamaica in November, and Fahay (1975) and Laroche (1977) recorded larvae off Georgia in July and August. Erdman (1976) found ripe fish from February through June in the northeastern Caribbean.

In this paper we describe the seasonality, spawning frequency, sex ratio, age and size at maturity, and fecundity of the vermilion snapper and discuss possible adaptive strategies for its reproduction.

The study area (Cape Hatteras, N.C., to Charleston, S.C.) was stratified by depth (i.e., inshore and offshore, the dividing depth being 55 m), and specimens were collected throughout. Most fish were obtained from the recreational fisheries throughout the Carolinas; however, some specimens were collected by hook and line or trawl from

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[3]Headboats are recreational fishing vessels which charge anglers for a day's fishing on an individual, thus "per head," basis.

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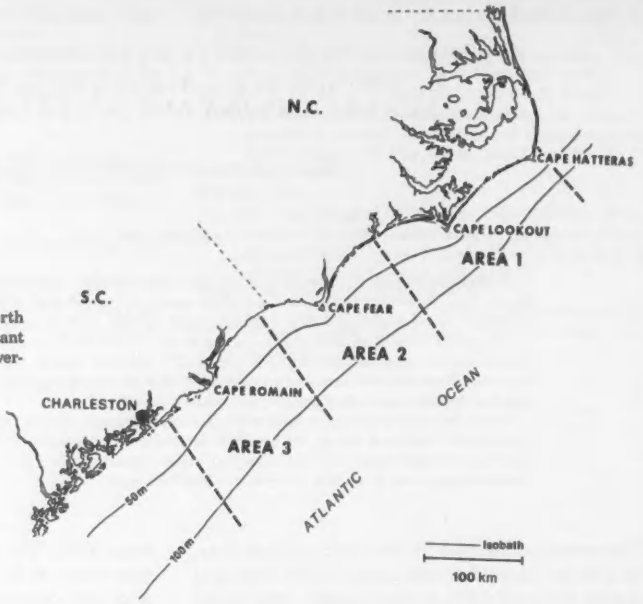

FIGURE 1.—Continental shelf off North Carolina and South Carolina and important bathymetric features that relate to the vermilion snapper study.

the RV *Onslow Bay* and the RV *Eastward*; most juveniles were trawled from RV *Dolphin*.

Temperature was taken by expendable bathythermograph, and photoperiod was obtained from the National Ocean Survey tide tables (U.S. Department of Commerce 1971, 1972, 1973). Specimens were weighed (nearest gram) and measured (nearest millimeter). Gonads were removed, preserved in 10% Formalin[4] for at least 1 wk, washed in tap water for several days, and then placed in 70% isopropyl alcohol. Frequency distributions of ovum diameters were plotted by month to determine seasonality, frequency, and duration of spawning (Hickling and Rutenberg 1936; Fahay 1954). The diameters of approximately 100 randomly selected ova from each of two females per month were measured to the nearest 0.05 mm by dissecting binocular microscope at 25×. To validate measuring ova from any portion of an ovary, we determined by analysis of variance that ova sizes were distributed uniformly (indicating uniform development) throughout the ovaries (Table 1).

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Later, the gonads were removed from preservative and weighed (nearest 0.1 g) after surface moisture was absorbed by blotting.

A gonosomatic index was used as a measure of reproductive development (Finkelstein 1969) for determining spawning seasonality and maturity. The index was calculated according to the formula $KG = W/TL^3$ where KG = gonad index, W = preserved (blotted dry) gonad weight in grams, TL = total length in millimeters. We realize that assuming the cubic relationship is arbitrary. Quast (1968) has shown for kelp bass, *Paralabrax clathratus*, that the percentage of body weight contained in gonads increases with fish length. Therefore, the true exponent is undoubtedly >3, but data limitations preclude more accurate formulation.

Ovaries used for fecundity studies were preserved in modified Gilson's fixative (Bagenal and Braum 1968). The ovarian tunic was removed and washed free of adhering ova. Additional washings separated developing ova from undifferentiated oöcytes and follicular material. A small subsample of ova (about 1,000 or less) was stored wet for later counting in a gridded Petri dish under a binocular dissecting scope. Subsamples and origi-

TABLE 1.—Analysis of variance testing the hypothesis that there is no difference in ovum diameters between anterior, posterior, and center sections of ovaries from three vermilion snapper. NS = not significant.

Fish no.	Source of variation	df	MS	F
1	Between sections	2	1.0769	0.46 NS
	Within sections	309	2.341	
2	Between sections	2	0.5417	0.97 NS
	Within sections	309	0.5770	
3	Between sections	2	29.907	1.09 NS
	Within sections	309	27.3512	

nal ova samples (total sample minus counting subsample) were drained and dried for 24 h at 40° C. Subsample and original ova sample dry weights were determined to 0.001 g on a beam balance, and the sum of these two weights provided the total ova sample dry weight. Fecundity was determined by proportionality where:

$$\frac{\text{fecundity}}{\text{total ova dry weight}} = \frac{\text{number of ova in subsample}}{\text{subsample dry weight}}.$$

Fecundity models were fitted by semilog transformation (log fecundity $= a + b \times$ length, weight, or age) and regressions are the functional regressions of Ricker (1973). The semilog formulation of fecundity models was used instead of more traditional log-log models because they fit the data best.

RESULTS

Seasonality, Frequency, and Duration of Spawning

Several lines of evidence indicate that spawning occurs from late spring through early fall. Males and females with ripe-appearing gonads were collected from late April through September, but few females were collected with ova loose within the ovarian tunic. Microscopic examination of preserved ovaries showed three types of maturing ova present during this period (in addition to maturing ova, undifferentiated transparent oöcytes were present and were by far the most numerous): the smallest developing ova (0.11-0.2 mm in diameter) were translucent and were the most numerous developing type; the next largest ova (0.33-0.43 mm in diameter) were nearly opaque throughout and less abundant than the preceding; the largest developing ova (0.46-0.71 mm in diameter) were typical mature teleost eggs with opaque cytoplasm occupying one pole of the egg which also contained transparent to translucent yolk material and oil globules. We observed these most mature ova only in ovaries collected from May to September, although what appeared to be ripe ovaries were also seen in April; furthermore, these mature ova occurred in only 7 of 149 ripe-appearing ovaries examined.

Frequency distributions of maturing ovum diameters (Table 2) show at least two size modes of ova present from April to October (three were present in one of two June samples), while only one smaller size mode or undifferentiated oöcytes were present in November, December, and March. No ova collected in January or February were examined. These data indicate spawning begins in late April or May and continues through September or perhaps early October.

Monthly mean gonad index values for 101 sexually mature females, sampled from May 1972 to April 1974, also denote late spring to fall spawning (Figure 2). No fish were collected in January or February 1973 or 1974; however, adult females collected in February 1975 had gonad index values of 0.51 and 0.40 which are consistent with gonad index trends indicated in Figure 2. Increasing

TABLE 2.—Developing ovum diameter-frequency distributions (percent) from two female vermilion snapper that were examined during various months of the study.

0.08 mm interval (midpoint)	1972 May	June	July	Aug.	Sept.	Oct.	Nov.	1973 Mar.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	1974 Apr.
0.06				1													
0.14	40	45	39	29	35				35	16	17	28	19	80	100		26
0.22	27	13	32	15	8				21	48	22	36	38	12			17
0.30	11	7	7	2	1				10	5	5	11	16				14
0.38	11	10	6	9	12				5	9	17	10	13	6			13
0.46	4	25	2	8	41				28	15	36	9	13	2			27
0.54	4		1	13	3				1		3	6	1				3
0.62	3		5	23								2					
0.70			8							4							
0.78										2							
Total	194	198	172	214	227				179	199	209	200	197	100	100		200
Mean, mm	0.25	0.27	0.27	0.37	0.32	—	—	—	0.28	0.29	0.34	0.27	0.27	0.17	0.14	—	0.3

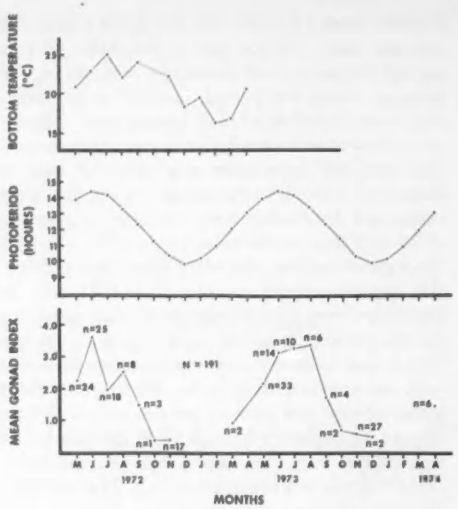

FIGURE 2.—Monthly mean gonad index of female vermilion snapper collected from May 1972 to April 1974, mean bottom temperatures at collecting sites, and photoperiod (U.S. Department of Commerce 1971, 1972, 1973).

monthly mean gonad index is well correlated with lengthening photoperiod and increasing bottom temperature.

The seasonal occurrence of juveniles and the large size variation within the youngest age-group provides additional evidence of an extended summer spawning season. During October and November 1973, several hundred juveniles ranging from 53 to 227 mm TL were trawled in Long Bay, N.C. and S.C., and also off Charleston. Aging of these fish from scales showed the sample to contain mostly age-groups 0 and 1. Using the growth rate for the first year of life (Grimes 1978) for extrapolating backwards, we determined that the age 0 fish collected in October and November 1973 were spawned throughout the summer months.

Although actual spawning was never observed, it probably occurs around rough bottom from 31 to 91 m but may be more concentrated in deeper areas (55-91 m). Ripe fish were taken over rough bottom at depths of 31-91 m when bottom temperatures were 20.6°-24.8° C. In Raleigh Bay and northern Onslow Bay, ripe fish were more abundant from 55 to 91 m; however, in the southern portion of the study area (southern Onslow Bay and Long Bay) ripe individuals were more equally distributed with depth.

Reproductive synchrony within schools may be indicated by hook-and-line sampling. Fish were usually caught in sudden bursts of fishing activity; seldom were single individuals encountered. Gonad indices for fish of similar size caught over a short time interval (probably from the same school) were nearly identical, indicating that reproduction within schools may be highly synchronized.

Multiple spawnings each season are indicated by the relative abundance of ova types (described earlier) at different times during the spawning season (Table 2). Maturing ova were present April through October and spawning apparently takes place during this period. Early in the spawning season (May) all three developing ova types were present in considerable abundance. When ripe ova were present later in the season (June or July), fewer smaller developing ova occurred. In August and September (late in the spawning season) when ripe ova were present, smaller developing ova were absent. The total of the developing ova types may represent all that will be spawned that season, and at each spawning a female develops only as many ova as her abdominal capacity will allow. This process could be repeated a number of times during the season until all eggs are spawned.

Variation in gonad index during the spawning period for similar size fish may also indicate fractional spawning. This was evident during the spawning months of 1972 and 1973 when the gonad index of both males and females of similar size varied by as much as a factor of 12 (Figure 3). The small size of ripe gonads combined with high fecundity (see subsequent discussion) is additional evidence for fractional spawning. The mean percent of body weight (observed) for ovaries of mature females collected during spawning months was 2.4% (0.6-5.8%, n = 40). Mature males had testes averaging 1.1% of body weight (0.4-2.4%, n = 15) during the same months. Also, we frequently observed semiflacid ovaries with no loose ova (perhaps partially spawned) in large adult females from June through September.

Maturation

Age and growth data of Grimes (1978) and our reproductive data indicate that most fish attain sexual maturity during their third or fourth years of life (186-256 and 256-324 mm TL), but a few

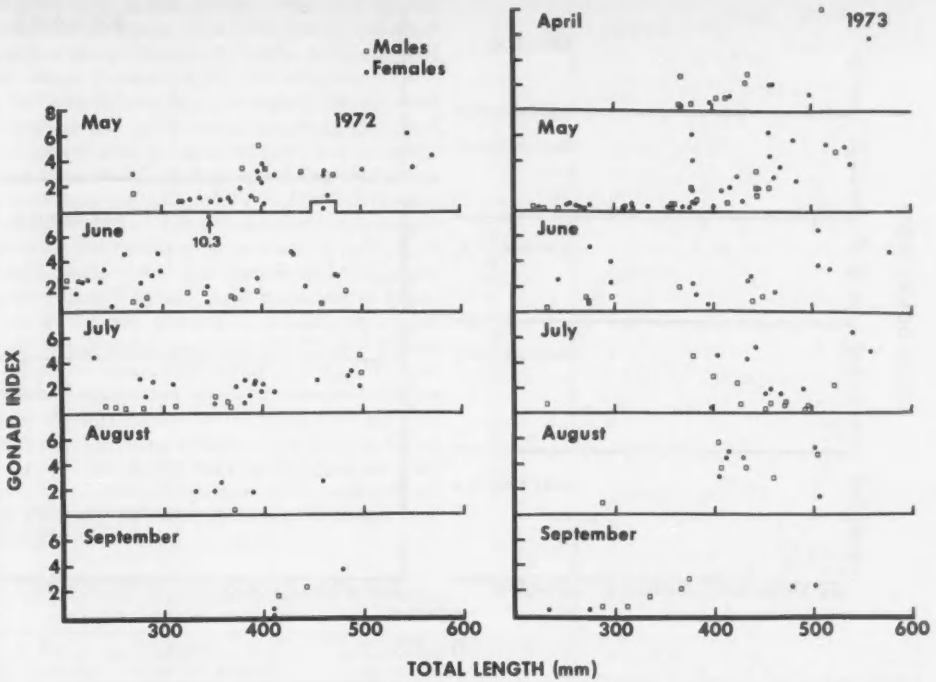

FIGURE 3.—Individual gonad index (gonad weight/(total length)^3) values for vermilion snapper over the spawning months of 1972 and 1973 plotted against total length.

precocious individuals may mature in their second year (100-186 mm TL) at about 150 mm TL. We determined age and size at maturity by examining a plot of monthly mean gonad index of females collected in the spawning season (June-September) by total length (Figure 4). Furthermore, spawning season (April-September) gonad index values for males and females (Figure 3) and monthly mean gonad index for each age-group of fish (Figure 5) show that fish age 4-9 (>324 mm TL) ripen earlier (April or May vs. June) and remained in reproductive condition longer (April to September vs. June to August) than younger spawning fish.

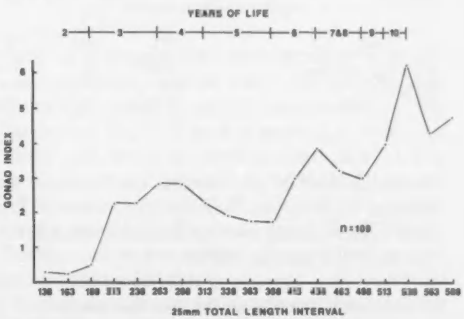

FIGURE 4.—Mean gonad index plotted by 25 mm TL intervals for female vermilion snapper during the spawning season (June-August). Approximate size at age was determined from Grimes (1978).

Sex Ratio

Sex ratio varies significantly from 1:1. From 1972 to 1974 we sexed 874 fish; 546 (62.5%) were females and 328 (37.5%) were males (1 df; χ^2 = 54.4; $P<0.001$). The total sample was analyzed by year of collection and sex ratios were judged significantly different from 1:1 in all years (Table 3). Higher proportions of females (62.5%) were col-

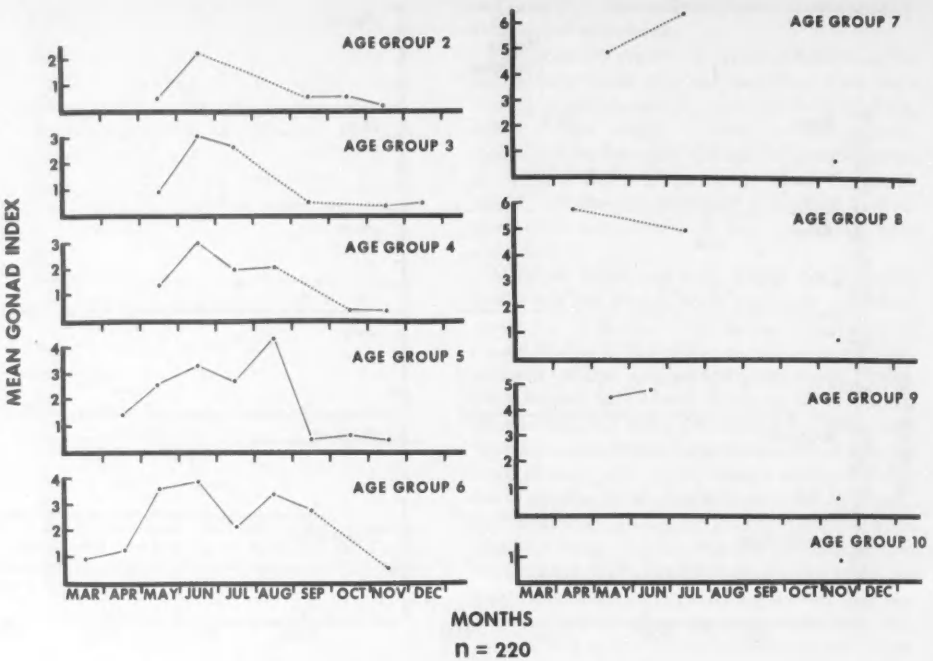

FIGURE 5.—Monthly mean gonad index (gonad weight/(total length)^3) for female vermilion snapper by age-group.

TABLE 3.—Test of the hypothesis that sex ratios of vermilion snapper did not vary significantly from 1:1 within years of collection.

Item	1972	1973	1974
Percentage of females	71.9	59.4	62.5
Sample size	135	424	315
Chi-square value	25.8*	15.1*	20.8*

*$P<0.01$.

TABLE 4.—Tests of the hypothesis that sex ratio of vermilion snapper did not vary significantly from 1:1 within 50 mm TL intervals.

Total length (mm)	n	Females (%)	Chi-square	Total length (mm)	n	Females (%)	Chi-square
101-150	105	49.5	0.0096	401-450	102	63.8	7.19*
151-200	117	63.4	8.83*	451-500	60	61.7	3.27
201-250	68	49.3	0.014	501-550	58	69.2	7.69*
251-300	99	61.2	4.94*	551-600	32	89.3	17.28*
301-350	90	59.4	3.38	601-650	1	100	
351-400	142	65.9	12.7*				

*$P<0.05$.

lected at shelf break habitats than inshore live bottom (60.5%), but the hypothesis that sex ratio and capture depth were independent was not rejected ($\chi^2 P>0.05, n = 852$).

There is a significant difference in sex ratio throughout the life of the fish (as estimated by total length); however, differences within some size intervals were not judged significant (Table 4). Contingency-table analysis showed that sex ratio and size were dependent ($\chi^2 P>0.05$, df = 9) (i.e., with growth sex ratios were different from 1:1 and changed significantly). In small fish (101-150 mm TL) the number of males and females was nearly equal, but at 151-200 mm TL the percentage of females increased to about 60%, where it remained somewhat stable until 501-550 mm TL, when percentage of females began to steadily increase (Table 4). Only one fish >600 mm TL was collected (618 mm) and it was a female.

Fecundity

Estimates of fecundity ranged from 8,168 to 1,789,998 ova for 41 females ranging from 229 to 557 mm TL (3-8 yr old and 136-2,293 g). Because

females may spawn several times per season, fecundity estimates were from ovaries collected early in the spawning season (May and June) and all classes of maturing ova were counted.

In Table 5, fecundity was separately regressed on total length (millimeters), weight (grams), and age (years) and, as expected, fecundity increases as a function of all three correlates. Fecundity increases so markedly in larger (older) fish (Figure 6) that semilog models were needed to adequately describe the relationship between fecundity and length, weight, and age. Length and weight are approximately equally good predictors of fecundity (r = 0.864 and 0.863, respectively). First spawners probably are about 205-275 mm TL and produce between 16,800 and 41,700 eggs. This estimate assumes that spawning extends from late June through September for young fish (age 2-4), that first spawning occurs in the third or fourth year (186-256 or 256-324 mm TL), that scale annuli form in March (Grimes 1978), and that approximately 25% of annual growth occurs from annulus formation to late June.

TABLE 5.—Functional equations for fecundity in vermilion snapper. Age (A) determined from scales.

Predictor	Equation	r	n
Total length (mm)	$F = \exp(7.07 + 0.013TL)$	0.863	41
Age (yr)	$F = \exp(7.57 + 0.873A)$	0.853	41
Weight (g)	$F = \exp(10.21 + 0.002W)$	0.864	41

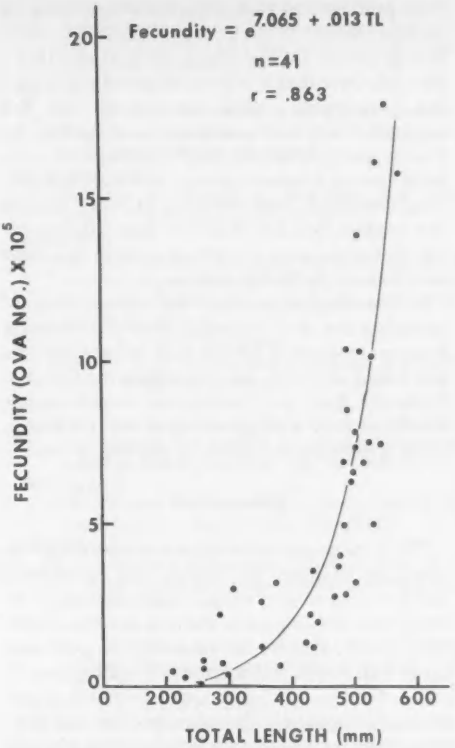

FIGURE 6.—The relationship of fecundity to total length of female vermilion snapper.

DISCUSSION

Spawning Seasonality

The conclusion that spawning occurs from late April through September is corroborated by Longley and Hildebrand's (1941) statement that spawning took place in summer around the Tortugas. Powles[5] and Fahay (1975) reported that larvae were collected at the surface off South Carolina and Georgia in June and July, and Laroche (1977) described a larval series collected off Georgia in August. Walker (1950), however, reports collecting vermilion snapper in spawning condition off North Carolina in February. Erdman (1976) sampled 400 vermilion snapper in the northeastern Caribbean and found fish in spawning condition January through June. Monroe et al. (1973) collected a ripe female in November off Jamaica and suggested, on the basis of these and more extensive data for other reef species, that spawning probably occurs year-round in the Caribbean, but that peak spawning is in winter where surface temperature is about 26.5° C. The larvae reported on by Fahay (1975) and Laroche (1977) were collected at 27° and 26.5° C, respectively, and we collected ripe fish off North Carolina when sea surface temperature was between 26° and 27° C.

It appears that spawning of vermilion snapper off North Carolina and South Carolina is restricted to warm months (late April or May-September), yet spawning may occur almost year-round in the Caribbean (Monroe et al. 1973; Erdman 1976). Similar life history variations in response to local environmental conditions are reported by Leggett and Carscadden (1978) for American shad.

[5]H. Powles, Fishery Biologist, South Carolina Marine Resource Center, Charleston, S.C., pers. commun. May 1975.

Several authors report fractional spawning in marine fishes (Starck and Schroeder 1971; Beaumarriage 1973; de Silva 1973; Macer 1974). Our inference that variation in gonad index during a spawning month for similar size fish suggests fractional spawning is supported by Starck and Schroeder's (1971) findings on a related species, *Lutjanus griseus*, the gray snapper. They concluded, from variation of ovary lengths and weights from fish of similar size, that spawning probably occurs more than once in the same season in south Florida waters.

In the results, we described three types of maturing ova and concluded that they indicate fractional spawning, yet the most mature ova type was found only in a few ripe-appearing females. Evidently final ova maturation occurs nearly simultaneously with spawning so that the probability of catching a completely ripe fish is low.

Maturation

There are no published reports on maturation in vermilion snapper, but Starck and Schroeder's (1971) results on gray snapper agree closely. They wrote that females are mature at age 3 and 190-200 mm SL. Results for vermilion snapper also agree with Starck and Schroeder's findings that *L. griseus* females >375-400 mm SL probably spawn more times each year than smaller ones, and Mosley (1966) observed (from a sample of fish 223-456 mm SL) that early in the spawning season, smaller red snapper, *L. campechanus*, showed less gonad development than larger ones, perhaps indicating earlier spawning by larger fish. Also similar to our results, Quast (1968) showed earlier and longer seasonal gonad maturation with growth in kelp bass.

Earlier spawning by older fish can probably be explained via the interplay between somatic and gonad growth and maintenance. Sexual maturity marks diminished growth in many fishes (Hubbs 1926; Magnuson and Smith 1963; Iles 1974). Female vermilion snapper older than 5 yr (390 mm TL) are beyond the years of most rapid somatic growth (Grimes 1978) and undoubtedly can afford to put more energy into gonad development, even though the energy costs of maintenance are greater for larger fish as well.

Cohen (1976), using a theoretical mathematical model, predicts that if reproductive success depends upon maximizing reproductive biomass, the change in the fraction of reproductive growth (diminished somatic growth and beginning reproductive growth) will occur at a time and mass just prior to maximum growth rate. We used annual length increments and a length-weight relation (Grimes 1978) to derive annual increments in mass, so that we could evaluate how well vermilion snapper fit the optimal timing of reproduction model. The greatest annual growth increment (weight) occurs between age 6 and 7. Age 5, then, is the year of life the model predicts the growth change, and Figure 5 shows that fish age 5 and older reflect the growth change by maturing earlier and being mature for a longer time each reproductive season.

Sex Ratio

The literature on other lutjanids provides little help in interpreting our findings that sex ratios of vermilion snapper vary significantly from 1:1 overall, and throughout life (as measured by length). Camber's (1955) data on red snapper showed a greater proportion of males when small (200-400 mm TL) but a higher percentage of females among larger fish (400 mm TL). Mosley (1966) reported 56% males and 44% females among red snapper (200-400 mm TL). Bradley and Bryan (1974), however, reported a 1:1 ratio for 1,129 adult red snapper (no size range reported), and Starck and Schroeder (1971) gave a 1:1 ratio for 772 gray snapper (including small juveniles to adults).

Wenner (1972) suggested several possibilities to account for unequal sex ratios (i.e., differential mortality, growth, and longevity; sex reversal; sex difference in activity; and in or out migiration from sampling area by one sex). There is no evidence to support any of these explanations in vermilion snapper, except differential mortality and longevity. Our results show conclusively that relative numbers of females begin to increase (to about 60%) at about 250-300 mm TL, further increase to about 70% at 500-550 mm TL, and eventually reach 90% above 550 mm TL (Table 2). These results indicate that males experience greater mortalities above 250-300 mm TL, and Grimes (1978) demonstrated greater longevity for females (no male was older than 8 yr, but females reach at least age 10). It is interesting to note that differential mortality commences approximately coincidentally with the onset of sexual maturity.

Our fecundity estimates agree reasonably well with published results for other lutjanids. Starck

and Schroeder (1971) estimated fecundity for gray snapper and found a 354 mm SL female to contain about 550,000 ova. Using length conversion equations for vermilion snapper (Grimes 1978), the 354 mm SL is approximately equivalent to a 450 mm TL vermilion snapper which would contain about 410,000 ova.

ACKNOWLEDGMENTS

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OBSERVATIONS ON EARLY LIFE STAGES OF ATLANTIC TOMCOD, *MICROGADUS TOMCOD*

R. H. PETERSON,[1] P. H. JOHANSEN,[2] AND J. L. METCALFE[1]

ABSTRACT

In southern New Brunswick, tomcod spawn in streams from late December to mid-January. The benthic eggs hatch and newly hatched larvae drift to sea in mid-March to mid-April at which time ocean temperatures are beginning to increase. Larval migration to sea is probably aided by active swimming of larvae to the surface to fill the swim bladder, which must be filled within 24 hours of hatching. Photopositivity of the larvae may assist in guiding larvae to the surface.

Water content and specific gravity of eggs reared in 0‰ were 2.8 mg and 1.030. Eggs reared at 10-30‰ had about 2.3 mg water per egg. Specific gravity of eggs incubated in 10‰ was constant for 27 days (at 2°-4° C) at 1.038, then decreased to 1.033. This decrease is associated with water uptake of 0.5-0.6 mg per egg and elimination of salt. The specific gravity of eggs incubated in 20‰ declined linearly from 1.044 to 1.037, associated with accumulation of 0.2 mg of water and elimination of a greater salt load. The specific gravity of eggs incubated at 30‰ declined linearly from 1.049 to 1.045, associated with 0.1 mg water uptake and apparently insufficient salt elimination. Water uptake and salt excretion problems are minimized for eggs reared in freshwater, and under the experimental conditions described here. Normal development could not occur in continued exposure to 30‰. In natural spawning areas, the incubation medium is freshwater for most of the total cycle, with seawater invading the area only at extreme high tide. The salinity tolerance of tomcod eggs is compared with that of freshwater and marine fish eggs in general.

Calculation of specific gravity of egg solids may prove a useful indirect way to investigate salt regulation in fish eggs.

The Atlantic tomcod, *Microgadus tomcod* (Walbaum), is an anadromous species of coastal streams from Newfoundland to Virginia. Adults ascend the lower reaches of southern New Brunswick streams in December and January. These spawning migrations form the basis for a recreational ice fishery in some larger rivers. An annual commercial catch of about 200 t is said to be taken from inshore waters of the northwest Atlantic (Scott and Crossman 1973). Local dip net fishermen take numbers of spawners for both human and animal consumption.

Details of the life history of the early stages (e.g., time of hatching, time of descent into saltwater) have been little studied. Leim (1924) observed that eggs would hatch in freshwater or saline water, but larvae would survive only in saline water. Booth (1967) found sperm motility to be maximal in low salinities, and that salinities of 0-15‰ permitted the highest percentages of eggs to develop to the blastula stage. Howe (1971) described the food habits and growth rates of young tomcod in the Weweantic River estuary, Mass.

The early stages of tomcod development have not been studied extensively; therefore, field studies were performed to obtain information on spawning habitat, rates of egg development, and timing of larval descent to saltwater. Tomcod eggs are deposited in areas subject to variable salinities, so the embryonic development and water balance of tomcod eggs reared in several salinities were also investigated to see how the responses of this species compare with those of freshwater and marine species.

METHODS

Field Studies

The mouth and estuary of Frost Fish Creek (frost fish is a local name for tomcod) were chosen as a study area because the stream hosts a large and regular spawning migration of tomcod which is undisturbed except for some local dip net fishing. It is a small stream (2-4 m wide) forming a common estuary with the Digdeguash River in

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southwestern New Brunswick, with a midsummer discharge ca. 80 l/s and a drainage area of 570 ha (Symons and Martin 1978; Symons and Harding[3]). The drainage basin is typical spruce-fir boreal forest with no human habitation. Portions of it farther upstream have been recently logged.

Tomcod spawn in a 10 to 15 m stretch at the head of tide in Frost Fish Creek (Figure 1). This area is freshwater for most of the tidal cycle, but has a variable bottom salinity (depending upon the height of the particular tide) during high tide. Extreme neap tides do not invade the spawning area. The stream substrate in the spawning area varies from ledge to boulders and cobbles. Most of the eggs settle in substrate interstices.

[3]Symons, P. E. K., and G. D. Harding. 1974. Biomass changes of stream fishes after forest spraying with the insecticide fenitrothion. Fish. Res. Board Can. Tech. Rep. 432, 47 p. Fisheries and Environmental Sciences, Fisheries and Oceans Canada, Biological Station, St. Andrews, NB E0G 2X0.

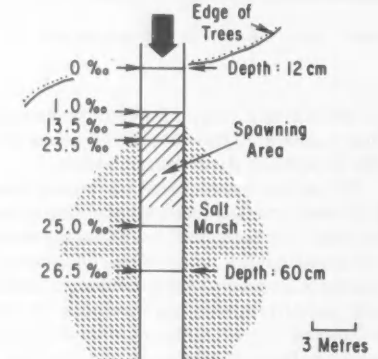

FIGURE 1.—Diagram of tomcod spawning area in Frost Fish Creek in the Digdeguash River estuary, New Brunswick. Depths and salinities are for a "typical" high-tide situation. Salinities were measured at the stream bottom. Hatched area indicates spawning area.

Drift samples were installed downstream of the area of egg deposition (Figure 1) near cessation of spawning (26 Dec. to 2 Jan.) to sample egg and larval drift. The samplers consisted of a galvanized-metal funnel, the narrow opening (5 × 20 cm) facing upstream, with a cloth bag attached to the downstream end (10 × 20 cm). The eggs and larvae accumulated in a 250 ml plastic beaker, with a screened, 2.5 cm diameter hole in one side, clamped to the bag. The sampler was threaded onto an iron rod driven into the stream bottom. A meter stick was installed to measure stream water levels, and stream salinities were measured with a salinity meter. Stream temperatures and drift samples were taken twice weekly at low tide, with the numbers of eggs collected averaged on a per-day basis. Eggs and larvae sampled were preserved in 10% Formalin[4] or 70% ethanol, those preserved in Formalin being cleared later (Galat 1972) to determine degree of development.

One sample of eggs was taken from the area of egg deposition with a Surber sampler in January 1977 to see if development of drifting eggs was the same as those that were not.

Egg Collection

Adults (1 female:2 males) anaesthetized in MS-222 were stripped of eggs and milt in the field. Immediately, the eggs were fertilized by the "dry" method and were washed with stream water 30 s after mixing (temperature at fertilization near 0° C). This water was fresh and was taken from a part of the stream where tomcod were spawning at the time (although spawning may continue into high tide conditions when the water would be of variable salinity). After 1 min the water was changed, and the bottle of eggs was packed in ice and transported to the laboratory. The eggs were transferred to the various incubation salinities 30 min after fertilization. The eggs are weakly adhesive initially, but this adhesiveness disappears if the eggs are separated.

Laboratory Studies

Eggs were incubated in columns of PVC pipe and fittings holding 190 ml of water (Figure 2). Screened floors and lids retained eggs and larvae. Water flowed through the columns at 100 ml/min

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

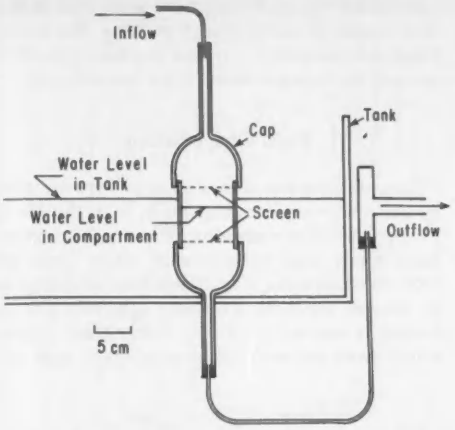

FIGURE 2.—Diagram of incubation chambers used to rear tomcod eggs.

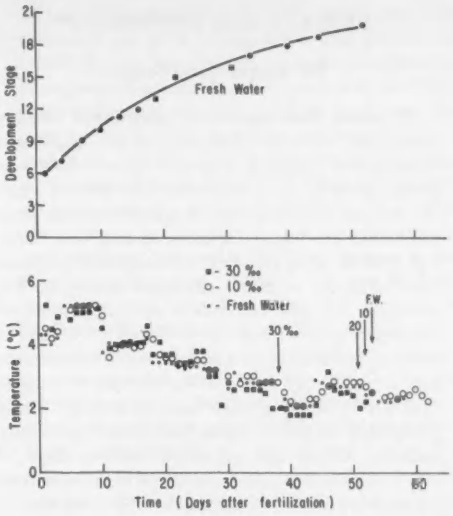

FIGURE 3.—Developmental stages and incubation temperatures for laboratory experiments on tomcod development. Upper panel: Appearance of developmental stages of tomcod eggs incubated in freshwater. Lower panel: Incubation temperatures for tomcod eggs at various incubation salinities. Arrows indicate median hatching dates at each salinity.

(range, 91-111). The columns were immersed in a freshwater bath cooled (2°-4° C) by recirculation of water to refrigerated header tanks. Water flowing to the columns passed through titanium coils in the bath. Water temperature decreased from 4.5° C at the beginning of January to 2.0° C in mid-February (40-d postfertilization), then increased to 2.5° C by the end of February (Figure 3). Eggs were incubated in salinities of 0 (2 columns), 10.1±0.3 (1 column), 20.2±0.6 (1 column), and 30‰ (2 columns). About 250-300 eggs were incubated in each column. Temperature and salinities, by conversion of specific gravity of water with Knudsen's (1962) hydrographical tables, were measured daily.

Columns were checked for egg and larval mortalities every 2-3 d. Every third day, three eggs were removed from each salinity and preserved in 10% Formalin for subsequent study of degree of development. About 100 newly hatched larvae were measured (±0.1 mm) from each salinity and the percentage of deformed larvae noted.

Water content of 10 eggs (combined) from each salinity was measured every fifth day by measuring loss of weight after drying for 16 h at 40° C under vacuum. Specific gravities (sp. gr.) of eggs were measured by glycerol flotation at 10° C as described by Peterson and Metcalfe (1977). Specific gravity of egg solids was calculated from total sp. gr. and water content where solid sp. gr. = egg dry wt/(egg vol. − vol. H_2O), egg vol. = wet wt/sp. gr., and vol. H_2O = water content/sp. gr. of H_2O. Egg diameters were measured microscopically to the nearest 10 μm. Buoyancies of newly hatched larvae, due to air content of the swim bladder, were measured by a Cartesian diver technique (Saunders 1965).

Photic responses of larvae were observed by placing groups of five larvae in a Petri dish, half of which was painted black, on a finger bowl full of ice. Uniform overhead illumination was used.

Statistical Procedures

Differences in water content and dry weights among eggs incubated in the various salinities were tested by one way ANOVA with individual differences detected by means of Duncan's Multiple Range Test. Changes in water content and dry weights during larval development were analyzed by linear regression methods.

RESULTS AND DISCUSSION

Developmental Stages

To assess development of eggs under natural conditions, a series of embryological stages was constructed (Table 1; Figure 3, lower) based on systematically sampled, laboratory-reared eggs. We attempted to make them consistent with those published previously for other species (e.g., Bonnet 1939 for Atlantic cod), although comparisons were difficult in more advanced embryos. For example, Atlantic cod lack a well-differentiated lower jaw at hatching, but it is well developed in tomcod. The stages are also referred to comparable figures in Hardy (1978:278-289) where possible (Table 1). Sampling eggs more frequently would have been useful in some instances; e.g., many anatomical features appeared between days 10 and 13, and are grouped into stage 11. The earliest stages were missed by taking the first sample at 24 h. Stages 3-6 were observed from field samples.

TABLE 1.—Summary of development stages and day of first appearance of anatomical features for tomcod eggs incubated at different salinities. For temperature regime see Figure 3. The stages are for eggs developing in freshwater. Stages 3-5 and 9 were observed in field-collected material only.

Stage	Description	Day of first appearance at: 0‰	10‰	20‰	30‰	Corresponding stage designation by Hardy (1978)
1	Prior to first cleavage	<1	<1	<1	<1	—
2	2 cells	<1	<1	<1	<1	168B
3	4 cells	<1	<1	<1	<1	—
4	8 cells	<1	<1	<1	<1	168C
5	16 cells	<1	<1	<1	<1	—
6	Large celled morula	<1	<1	<1	<1	168E
7	Small celled morula	4	4	4	4	168H
8	Embryonic axis	7	7	7	7	168J
9	Küpfer's vesicle and first somite	—	—	—	—	168E
10	Notochord	10	10	10	10	—
	Optic vesicle	10	10	10	10	169G
11	Eye lens	13	13	13	16	169K
	Ear placode	13	13	13	16	—
	Pericardium	13	13	13	19	—
	Brain lobes differentiating	13	13	13	22	—
	Fin fold	13	13	13	16	—
12	Pectoral fin buds, axial pigmentation	16	16	16	28	170E
13	Eye faintly pigmented	19	19	19	19	170G
14	Gill slit	22	22	22	22	—
	Swim bladder	22	22	25	28	—
15	Nasal placodes	25	25	31	none	—
16	Beginning of pronounced snout	31	31	31	none	171A
17	Lower jaw, mouth not opened	34	34	34	34	171B
18	Mouth can be or is open	37	37	37	—	171C
19	Pigment on lower jaw	45	46	—	—	172A
20	Hatching	—	—	—	—	172A

Irregularities in development were seen in the later stages of development at 30‰. The snout failed to develop normally, and the development of pectoral fin buds and brain lobes was delayed.

Field Observations

Largest numbers of tomcod eggs were sampled by the drift samplers (Figures 4, 5) in the 15- to 20-d period after spawning. The numbers correlated fairly well with stream water level for 1977-78 when water levels were measured (Figure 5). Largest numbers of drifting eggs may also be related to spawning activity rather than stream water levels per se. Typical numbers of eggs col-

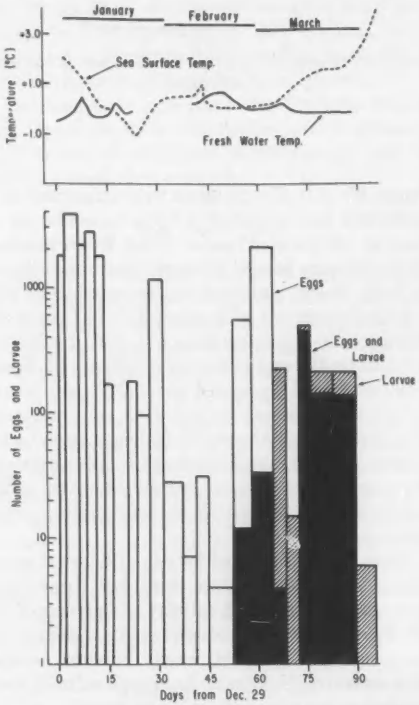

FIGURE 4.—Movements of tomcod eggs and larvae out of Frost Fish Creek. Upper: Environmental conditions and numbers of sampled tomcod eggs and larvae are shown for the 3 mo of egg and larval stream residence in 1976-77. Freshwater temperatures (solid line) and sea surface temperatures (dashed line) for January-April 1976-77. Lower: Histogram of numbers of tomcod eggs and larvae caught in drift samplers. Open bars, eggs; solid bars, eggs and larvae; hatched bars, larvae.

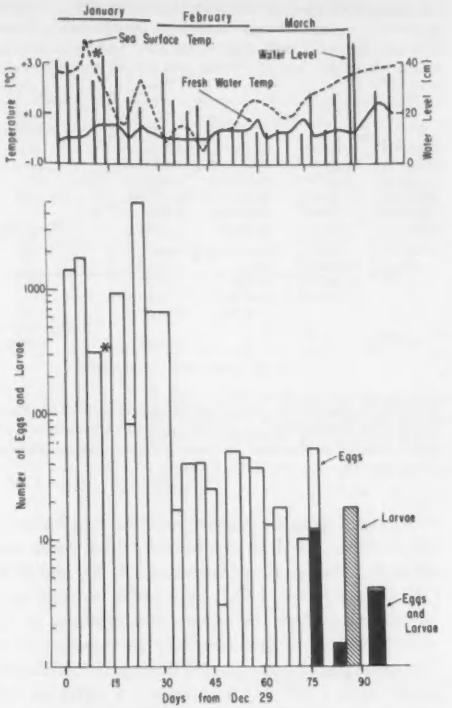

FIGURE 5.—Similar to Figure 4 but for 1977-78. Upper panel includes water levels (vertical bars). Asterisk indicates occurrence of a winter freshet, at which time drift samplers were washed out.

lected ranged from a few hundred to a few thousand per 24 h during these first 15-20 d. In mid-February, stream flow rates decreased as the precipitation accumulated in snow and ice. Typical numbers of eggs sampled/24 h during this period were 10-100. Hatching occurred in March and April (Figures 4, 5). Larvae began to be captured somewhat earlier in 1976-77 and were taken in greater numbers than in 1977-78. This latter phenomenon is thought to be because the sampler was totally submerged in 1977-78, whereas part of it was emergent in 1976-77. Larvae probably emigrate into saltwater near the surface immediately after hatching, as will be discussed in a later section and may have passed over the submerged sampler in 1977-78. Some of the earliest larvae may have hatched in the samplers as a result of warming on the return to the laboratory. These larvae appeared normal and viable. The hatching period in nature corresponded to rising stream water levels in late March in 1977-78. Sea surface temperatures had also risen to 3.0°-4.0° C during fry emigration. Catches of larvae terminated in early to mid-April of both years.

The earliest stages of development obtained in the drift samplers were stage 3 and 4 eggs (Figure 6), owing to lag from spawning to sampling. By the third week of January the embryonic axis was discernible in most eggs sampled. By mid-February, eyes and body axis had become pigmented, nasal placodes and fin fold were appearing, and the tail had curled past the posterior

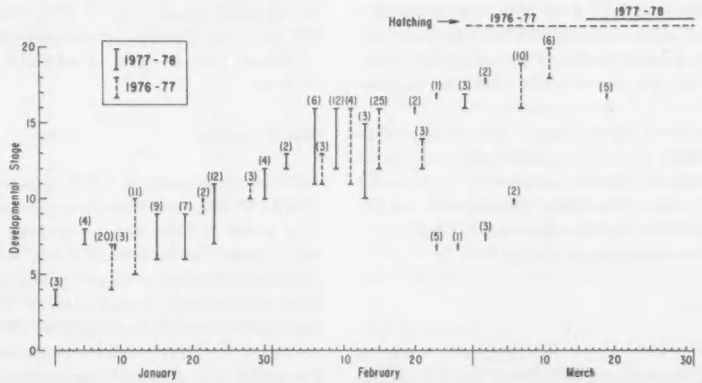

FIGURE 6.—Stages of embryonic development for eggs sampled from Frost Fish Creek with drift samples in 1976-77 and 1977-78. Vertical bars indicate ranges of development observed. Numbers of eggs inspected are in parentheses. Small arrows indicate samples where all eggs were at the same stage.

margin of the eye. Hatching began in late February to mid-March. A series of relatively early stage eggs was also obtained in late February to mid-March 1978 (Figure 6), indicating a possible second spawning of tomcod in late January to early February.

Laboratory Observations

Survival to Hatch and Length at Hatching

Tomcod egg survival to hatching was highest in freshwater (Table 2). Fifty-eight percent of the freshwater eggs hatched, compared with 50, 37, and 13% at 10, 20, and 30‰ salinities, respectively. About half of the mortality at 0 and 10‰ occurred at about day 30 (stage 15). Above 10‰ high mortality also occurred at earlier stages of development.

TABLE 2.—Percentage survival to hatching, total larval length at hatching, and median time to hatch for tomcod eggs incubated at four salinities. Standard deviations are given for larval lengths.

Item	0‰	10‰	20‰	30‰
Percentage egg survival to stage 19	70	73	48	21
Percentage hatched	58	50	37	13
Mean length at hatching (mm)	7.56±0.69	7.25±0.31	6.31±0.44	—
Number of larvae measured	165	104	85	
Time to median hatch (d)	54	51	51	38

Larvae hatched in freshwater were significantly longer than those from higher salinities (7.54 mm for freshwater vs. 7.25 and 6.31 mm at 10 and 20‰, respectively). Larvae at 30‰ had severe spinal curvature and could not be measured accurately. Hatching was earlier at the higher salinities.

The developmental success of tomcod eggs varied with salinity, so various parameters associated with water balance were measured on eggs reared at 0, 10, 20, and 30‰. These parameters are all interdependent so that changes in one may result in concomitant changes in others.

Specific Gravity

The sp. gr. of freshwater (FW) eggs was constant throughout development (Figure 7) at 1.030, implying that weight and volume were not changing or that they were changing in such a way that the sp. gr. was constant. In contrast, eggs incubated at 20 and 30‰ decreased in sp. gr. throughout development. Specific gravity at 10‰ was constant for the first 25 d of incubation, then decreased linearly. The sp. gr. of water at 10, 20, and 30‰ (10° C) are 1.009, 1.017, and 1.024, so that eggs were denser than the incubation medium at all salinities and by approximately the same amount. For example, the sp. gr. of FW eggs is 1.030 compared with 1.000 for freshwater, a difference of 0.03 sp. gr. units. The sp. gr. of 20‰ eggs (extrapolated to 0 time at 20‰ from Figure 7) is 1.045 compared with 1.017 for the incubation medium, again a difference of 0.03 sp. gr. units. Changes in sp. gr. may be associated with changes in water content, loss of solids through metabolism, change of salt content of eggs, or a combination of these factors.

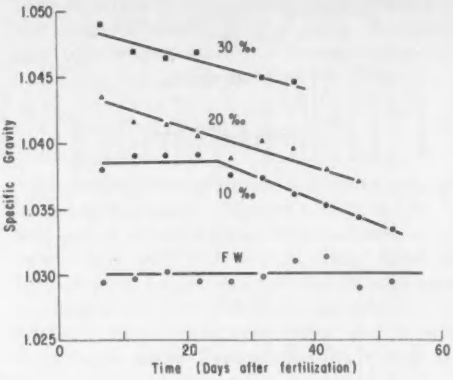

FIGURE 7.—Specific gravity of tomcod eggs incubated at various times from fertilization at various incubation salinities. Each point is based on the mean of measurements made on 10 eggs. Lines fitted by eye. FW = freshwater.

Water Content

Mean water content of FW eggs was 2.83 mg/egg (Table 3) with no trends throughout development. The water content and percentage water content of FW eggs for the first 27 d of development were significantly higher than the values obtained at the other incubation salinities ($P<0.05$, ANOVA, Duncan's Multiple Range Test). The percentage water content increased from 86.4 to 89‰ over the final 25 d of egg development, attributable to decreases in egg dry weight (Tables 4, 5).

There were no significant differences among the percentages of water content of eggs reared at the three higher incubation salinities for the first 27 d

TABLE 3.—Water content (milligrams per egg) and percentage water (parentheses) in tomcod eggs at various incubation salinities and days from fertilization. Each value represents 10 eggs. Sampling periods were fewer at 20 and 30‰ due to earlier hatch.

Days of incubation	0‰	10‰	20‰	30‰
9	2.86(86.7)	2.19(82.3)	2.50(84.7)	2.35(81.9)
12	2.87(87.2)	2.14(84.3)	2.48(83.5)	2.32(82.9)
17	2.72(86.6)	2.36(81.9)	2.47(83.4)	2.54(83.6)
22	2.94(85.5)	2.22(81.5)	2.39(83.9)	2.29(79.8)
27	2.78(86.1)	2.34(83.9)	2.30(82.7)	2.40(82.2)
27-d mean	2.83(86.4)	2.25(82.8)	2.43(83.6)	2.38(82.0)
32	2.78(86.8)	2.40(84.5)	2.41(84.0)	2.42(83.0)
37	2.87(87.5)	2.44(85.3)	2.44(84.5)	2.55(84.7)
42	2.86(89.4)	2.66(86.0)	2.60(86.1)	—
47	2.88(87.8)	2.58(85.4)	2.65(85.8)	—
52	2.76(89.0)	2.91(88.2)	—	—
Newly hatched larvae	1.41(85.5)	—	—	—

The water content of newly hatched FW larvae was 1.41 mg (85.5%), so about half of the water in the FW egg is associated with perivitelline fluid and zona radiata.

Dry Weight

No measurable change in egg dry weight occurred over the first 27 d of incubation (Table 4). A one way ANOVA indicated significant differences among the mean dry weights for the first 27 d of incubation ($F = 3.9$, $P<0.05$). The mean dry weight of 30‰ was significantly greater than those of FW and 20‰ eggs (Duncan's Multiple Range Test).

TABLE 4.—Dry weights (mg) for various incubation salinities and times from fertilization (d). Each value is averaged from 10 pooled eggs. Values to the left of the bracket for the first 27 d of development are means for that period.

Days of incubation	Incubation salinity (‰) 0	10	20	30
9	$\pm^{0.45}_{0.03}$ { 0.44	$\pm^{0.47}_{0.05}$ { 0.47	$\pm^{0.47}_{0.02}$ { 0.45	$\pm^{0.52}_{0.04}$ { 0.52
12	0.42	0.40	0.49	0.48
17	0.42	0.52	0.49	0.50
22	0.50	0.50	0.46	0.58
27	0.45	0.45	0.48	0.52
32	0.42	0.44	0.46	0.51
37	0.41	0.42	0.46	0.46
42	0.34	0.40	0.42	—
47	0.36	0.44	0.44	—
52	0.34	0.39	—	—
Newly hatched larvae	0.25	—	—	—

TABLE 5.—Statistical parameters for regressions of percentage water content vs. time (d) and dry wt vs. time (data given in Tables 3, 4). Times are for days 27-52, inclusive. b = slope of regression equation, r = correlation coefficient, df = degrees of freedom.

Regression	Parameter	Incubation salinity (‰) 0	10	20
% H_2O vs. time	b(%/d)	0.10	0.17	0.13
	r	0.80	0.91	0.93
	df	4	4	3
	t	2.72	4.53	4.47
	P	~0.05	<0.025	<0.05
Dry wt vs. time	b(mg/d)	−0.0046	−0.0018	−0.0024
	r	0.96	0.70	0.83
	df	4	4	3
	t	3.55	3.92	2.60
	P	<0.025	<0.025	<0.1

of incubation. The water content of 10‰ eggs increased over the last 25 d of incubation at 0.023 mg/egg per d ($P<0.05$, Tables 3, 5), until the water content at hatching approached that of FW eggs. The 20‰ eggs took up water after 27 d incubation at 0.018 mg/egg per d ($P<0.01$), but the water content of these eggs was still lower than for eggs incubated in FW and 10‰. The 30‰ eggs may have taken up slight amounts of water, but the data are insufficient to be tested statistically.

Dry weight decreased significantly over the last 25 d (Tables 4, 5). This decrease was greatest in freshwater, about 0.1 mg/egg compared with 0.07 and 0.04 at 10 and 20‰, respectively. Although sample size is inadequate for statistical analysis, it would appear that the 30‰ eggs lost about 0.05 mg/egg. Yolk content of newly hatched larvae was not measured; however, larvae hatched from higher incubation salinities appear to have more yolk (Figure 8), an observation supported by the fact that hatching is earlier at higher salinities. The lesser amount of yolk of FW eggs is in agreement with the greater loss of solids by these eggs.

About 25% of the dry weight of FW eggs is lost at hatching, and is thus contributed by the chorion and the perivitelline fluid.

Egg Diameter

The diameters of 10 eggs from each incubation salinity were measured at the time intervals indicated in Table 6. There was no indication of any change in egg diameter with length of incubation (Table 6), so that the water uptake at the three

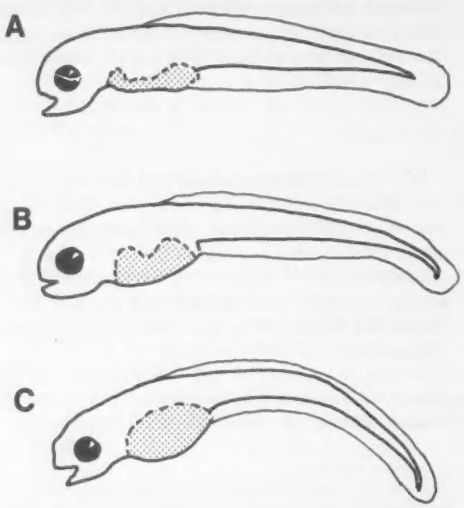

FIGURE 8.—Newly hatched tomcod larvae from various incubation salinities. Note the larger amounts of yolk remaining, the higher the salinity of incubation. A. Freshwater; B. 10‰; C. 20‰. Yolks have shrunk due to (Formalin) fixation effects. Magnifications 13×.

TABLE 6.—Egg diameters (millimeters) for various incubation salinities and incubation times. Each value is the mean of 10 measurements. v = calculated egg volume (microliters). Standard deviations given in parentheses.

Days of incubation	0‰	10‰	20‰	30‰
4	1.85(0.06)	1.79(0.08)	1.77(0.05)	1.81(0.09)
12	1.86(0.04)	1.76(0.07)	1.75(0.06)	1.76(0.04)
17	1.87(0.05)	1.75(0.05)	1.79(0.05)	1.80(0.04)
22	1.89(0.04)	1.77(0.05)	1.76(0.05)	1.78(0.05)
27	1.84(0.07)	1.75(0.05)	1.76(0.05)	1.76(0.04)
32	1.89(0.02)	1.74(0.05)	1.78(0.06)	1.78(0.05)
37	1.90(0.05)	1.77(0.05)	1.78(0.05)	1.78(0.06)
42	1.93(0.05)	1.82(0.04)	1.81(0.05)	—
47	1.84(0.04)	1.81(0.04)	1.76(0.06)	—
52	1.86(0.07)	1.79(0.05)	—	—
$\bar{x}$	1.87	1.78	1.77	1.78
v	3.47	2.86	2.84	2.83

higher salinities toward the end of the incubation period did not lead to measurable swelling, although slight swelling within experimental error probably occurred. The mean diameters of FW, 10, 20, and 30‰ eggs were 1.87, 1.78, 1.77, and 1.78 mm, respectively. The standard deviations for lots of 10 eggs varied from 0.02 to 0.09 mm, and were 0.04-0.05 in most cases. The greater diameter of the FW eggs is no doubt related to the higher water content of these eggs.

Specific Gravity of Egg Solids

The sp. gr. of FW egg solids (lipids included) was constant at 1.27 for the first 27 d of incubation (Figure 9), then rose linearly to about 1.36 just before hatching. This increase in sp. gr. of egg solids may be due to increase in compact tissue, such as cartilage. It could also reflect a rapid increase in embryonic tissue and a corresponding decrease in yolk solids. The sp. gr. of solids of Atlantic salmon alevins also increases during development (Peterson and Metcalfe 1977). This was shown to be due to increase in embryonic mass, the solids of which had a higher sp. gr. than did yolk solids.

The sp. gr. of 10‰ egg solids was identical to that of FW eggs throughout. Apparently, insufficient salt penetrated these eggs to change the solids' sp. gr. measurably. This apparent lack of difference between FW and 10‰ eggs should be accepted with some caution, since an error of 0.01 mg/egg in estimating dry weight (averaged over the first five measurements) could result in a shift in solids' sp. gr. by 0.2 units. Since the dry weight of 10‰ eggs was some 0.02 mg greater than that of FW eggs (Table 4), some salt may well have entered the 10‰ eggs.

The sp. gr.'s of egg solids for 20 and 30‰ eggs during early development were much higher than for the two lower salinities (Figure 9), and they

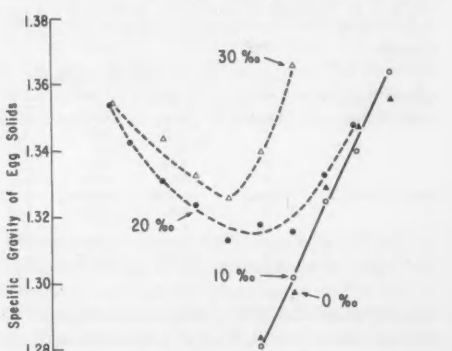

FIGURE 9.—The specific gravity of egg solids (as calculated from water content and egg specific gravity) at various times from fertilization for various incubation salinities. Lines fitted by eye.

decrease with time until a minimum is attained at 27 d postfertilization. The sp. gr. then rose again, as for eggs reared at 0 and 10‰. The decrease in egg solids' sp. gr. from fertilization to day 27 at 20 and 30‰ may be due to more efficient salt elimination as the embryo grows. After 27 d the decrease due to salt elimination is more than balanced by increases due to factors postulated above for FW eggs. Apparently, eggs reared at 20‰ were successful in eliminating salt, because the sp. gr. of their egg solids tends to converge with that for eggs reared at lower salinities. At 30‰, however, the embryos appeared to be unable to eliminate excess salt successfully because the solids' sp. gr. never approached those for eggs reared at lower incubation salinities. The 30‰ eggs hatch earlier than those incubated at lower salinities, perhaps in response to high salt concentrations. As mentioned previously, they were abnormally developed.

The higher sp. gr. of egg solids at 30‰ would require that 15% of the solids be excess salt (using the formula $1.27a + 1.8(1-a) = 1.35$; where a = proportion of egg solids that is not salt; 1.8 = sp. gr. of salt, 1.27 = sp. gr. of FW egg solids, 1.35 = sp. gr. of 30‰ egg solids). This amounts to about 0.08 mg. This is reasonably close to the increase in dry weight of 30‰ eggs over FW eggs (0.07 mg). The decrease in sp. gr. of 30‰ egg solids to its minimum of 1.33 would require the loss of 0.02 mg of salt.

Newly hatched larvae in freshwater that did not have access to the water surface had an sp. gr. of 1.032, which is nearly identical to that of eggs incubated in freshwater. If larvae were permitted access to air at the water surface, the sp. gr. declined within 7 h to 1.01, coincident with ingestion of air into the swim bladder. Newly hatched larvae were observed swallowing air at the surface. The filling of the swim bladder was investigated further with a Cartesian diver technique. Larvae that had access to air floated at a flotation pressure (Saunders 1965) of 154 mm Hg (130-170, $n = 6$) (0.8 atm). Those that had been denied access to air for 24 h failed to float at 675 mm Hg (645-685, $n = 15$), corresponding to 0.1 atm (the greatest vacuum attainable with the apparatus). No air was observed in the swim bladder of these larvae. These larvae were then allowed access to the surface overnight. When tested subsequently, none floated at 675 mm Hg, nor was air observed in the swim bladder. These latter larvae, unlike larvae with air in the swim bladder (that spend most of their time near the surface), stayed on the bottom of the container.

Newly hatched larvae were photopositive as tested in a half-blackened Petri dish. In two trials, 78% (39/50) and 64% (16/25) larvae were observed in the lighted (unpainted) half of the Petri dish. When the dish was kept in darkness, 46% (23/50) and 36% (9/25) larvae were observed in the unpainted half. Larvae were commonly observed to aggregate near the lighted sides of rearing containers.

GENERAL DISCUSSION

The changes that occurred in eggs reared in various salinities will first be summarized:

Eggs reared in freshwater consisted of 2.8 mg water, sufficient for the embryo's needs, being constant throughout development. The egg sp. gr. was also constant despite decrease in solid materials (ca. 0.1 mg)—the egg diameter should therefore decrease slightly (about a 1.7% decrease is required), although this was not observed, as it is within experimental error.

Eggs reared in 10‰ salinity have about 2.2 mg water for the first month of development, but take up an additional 0.5-0.6 mg in the later stages of development, due to the greater water requirements of embryonic tissue. Some of this uptake may also be associated with formation of fluid filled body cavities (Zotin 1965). This water uptake was associated with a decreased egg sp. gr. The 10‰ eggs may have a slight salt load which is probably eliminated in the later developmental stages. The egg dry weight declined by only 0.07 mg, and newly hatched 10‰ larvae may have larger yolks than do those in 0‰ (Figure 9).

Eggs reared in 20‰ salinity had a water content equal to or greater than that of 10‰ eggs in the early stages of development, but had to tolerate a higher salt load (ca. 0.04 mg/egg) as a result. Egg sp. gr. declined throughout development due to salt elimination as the embryo developed and to accumulation of about 0.2 mg water during the later developmental stages. Advanced embryos eliminated much of the initial salt load as the egg solid sp. gr. of late stage eggs is nearly identical to that of eggs reared at lower salinities. The concept of salt elimination seems reasonable, but is subject to some uncertainty in these experiments because the solids associated with the chorion and perivitelline fluid are included in the estimates of

solids sp. gr. These compartments of the egg obviously would have no capacity for elimination of salts. Egg dry weight declined by only 0.04 mg at hatching as newly hatched 20‰ larvae appear to have even more yolk than 10‰ larvae (Figure 8). The 20‰ curve in Figure 9 suggests that salt elimination began very early and increased as the embryo grew. It is probable that at least the early salt elimination had a cellular rather than organ basis.

Eggs reared in 30‰ salinity also had a water content similar to those reared at 10 and 20‰, but the salt load was high. Water accumulation during the later developmental stages was low (ca. 0.1 mg). The sp. gr. of egg solids goes down over the first 27 d of development, indicating some elimination of salt. The pattern during the later stages of development is strikingly different from that at 20‰ in that the solids' sp. gr. again rose to about 1.37 at 37 d of incubation at which point the larva hatched. Problems with salt balance and osmoregulation may have led to the deformities and early hatching. The dry weight of 30‰ eggs decreased only slightly during development.

It has been shown, for the eggs and larvae of some marine organisms, that the salinity in which fertilization and the earliest stage of development occur may influence development and growth of subsequent stages in the life history (Kinne 1962). It is therefore possible that eggs fertilized in water of higher salinity might have responded differently to the various experimental salinities. Booth (1967) obtained data suggesting that fertilization could occur in salinities as high as 15‰. It is notable, however, that the eggs of *Cyprinodon macularius* in Kinne's experiments were allowed to develop 3-6 h in the spawning salinity, and at a higher temperature (27° C) than was the case for the tomcod experiments. It is probable that the eggs of *C. macularius* had developed further before experimentation.

The tomcod's early life history seems adapted to the hydrodynamics of streams in which it spawns. Spawning migrations occur in late December to early January while water levels are still high from the fall freshets. The eggs develop throughout midwinter when water levels are low, thus minimizing loss of eggs from the stream, then hatch when water levels are rising coincident with the early snow melt. The higher water levels during hatching would ensure rapid flushing of larvae into the estuary. Newly hatched larvae probably rise to the stream surface soon after hatching and ingest air into the swim bladder, with possibly the positive response to light facilitating surfacing. This behavior of newly hatched larvae would also ensure rapid flushing into the estuary.

The continuous drift of eggs out of the stream is somewhat puzzling. Most eggs taken in the drift samples were alive and apparently developing normally. These perhaps are eggs which had been deposited where they were likely to be taken up into suspension. In support of this suggestion, egg drift was positively correlated with stream level. Whether these eggs continue to develop would depend in part upon the salinity conditions where they finally settle and the ambient salinity during earlier development. Laboratory results indicate that less than full salinities are required for normal development from fertilization, but the effects of variable salinities on tomcod egg development were not investigated.

The tomcod egg resembled those of freshwater species (rather than marine species) in regard to salt tolerance, assuming that the responses reported here are typical. Eggs of brook trout exhibit increased mortality above 6‰ salinity with total mortality at 12‰ (Sutterlin et al.[5]). Species such as *Abramis* will hatch in salinities up to 20‰, although 2.5-5‰ is optimal (Holliday 1969). With the tomcod, between 20 and 30‰ salinity appears to be the upper limit for production of normal larvae. By way of contrast, eggs of several marine species have been hatched in salinities up to 60‰ (cod, herring, plaice), although optima are usually in the 25-30‰ range (Holliday and Blaxter 1960; Holliday 1965).

Eggs of marine species tend to swell at low salinities (usually <15‰); above this salinity egg diameter is constant (Holliday 1965; Solemdal 1967). Tomcod eggs require salinities of <10‰ for noticeable swelling to occur.

Several parameters measured (water content, dry weight, solids' sp. gr., and egg sp. gr. for 10‰ incubation) begin to change dramatically at about 27 d of incubation. In relation to embryonic development it seems probable the embryonic mass is beginning to increase dramatically at this point, resulting in the noted physiological changes. Perhaps these changes are linked to the high mortality occurring at this stage of development.

[5]Sutterlin, A. M., P. Harmon, and H. Barchard. 1976. The culture of brook trout in salt water. Fish. Mar. Serv. Res. Dev. Tech. Rep. 636, 21 p. Fisheries and Environmental Sciences, Fisheries and Oceans Canada, Biological Station, St. Andrews, NB E0G 2X0.

Zotin (1965) reported that eggs of freshwater teleosts (e.g., loach, zander (*Lucioperca*)) took up no water after water hardening until the chorion began to stretch due to weakening by the hatching enzyme. The mullet egg took up water during the second half of development during which time the perivitelline space first appeared. With the tomcod, water uptake occurred in the latter stages of development in the three higher salinities. It is not known where this water was distributed within the egg, but it was probably incorporated into embryonic tissue.

It is inferred, from calculated specific gravity of egg solids, that tomcod embryos osmoregulated to some degree, becoming more proficient as development proceeded. This may be simply a function of embryonic size, resulting in more osmoregulating tissue. It has been suggested by Holliday (1965) that plaice embryos can regulate osmotic concentration after gastrulation, which occurs in 9 d or less in these tomcod eggs. Holliday (1969) also showed that flounder eggs could regulate yolk sodium from fertilization. Unfortunately, we did not make measurements here before 9 d of incubation.

Holliday and Blaxter (1960) and Forrester and Alderdice (1966) observed development to proceed faster at higher salinities for herring and Pacific cod, respectively. While tomcod hatched earlier at higher salinities, there is little suggestion that development occurred more rapidly. Rather, it appeared that the freshwater larvae grew larger prior to hatching. Some structures were delayed, or never appeared in 30‰ embryos, but this is due to abnormal development at this salinity. Abnormal development has frequently been recorded at abnormally high salinities. Usually the deformities are skeletal as are observed for tomcod, or involved body cavity deformities (Holliday 1965; Alderdice and Forrester 1971).

Although the tomcod is a physoclist species, the pneumatic duct is apparently functional in the newly hatched larva. In <24 h the duct is closed, and the larva can no longer fill the swim bladder by air ingestion. Larval loss of the pneumatic duct has been implied for physoclists generally (Harden Jones 1957). Whether or not the duct is utilized in initial filling of the bladder is apparently quite variable (Johnston 1953; Schwarz 1971).

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NOTES

OBSERVATIONS OF SEA OTTERS DIGGING FOR CLAMS AT MONTEREY HARBOR, CALIFORNIA

Although the feeding behavior of the sea otter, *Enhydra lutris*, is frequently observed from the surface, few underwater observations of foraging sea otters have been published. Faro (1969) and Houk and Geibel (1974) described the underwater behavior and tool use of sea otters when they removed abalone from rock substrates. Shimek (1977) observed a sea otter foraging for snails and presumably other invertebrates by patting the surface of rocks and feeling into cracks. Shimek also described a sea otter digging up the echiuroid worm, *Urechis caupo*, from a silt and cobble substrate. Further deductions about underwater foraging behavior have been made from collections of abalone shells with the characteristic "otter break" hole in the middle (Wild and Ames[1]) and from observations of aluminum beverage cans bitten by otters to remove octopus (McCleneghan and Ames 1976). Some sea otters can be enticed underwater to take food offered them (pers. obs). However, these latter observations of underwater food manipulation are of limited value because the otters also take items unpalatable to them (e.g., the holothuroid *Stichopus californicus*), and because the otters were clearly interacting with the diver observer. These accounts of underwater foraging indicate that sea otters use primarily tactile sensitivity of the forelimbs to locate and capture prey, whereas all other marine mammals (pinnipeds and cetaceans) use their jaws to capture prey. Radinsky (1968) hypothesized that the sea otter evolved forelimb tactile sensitivity separately from the aonychoid otters.

The large impact of sea otters on Pismo clam, *Tivela stultorum*, populations in California has been documented (Stephenson 1977; Miller et al.[2]), and in Prince William Sound, Alaska, 81% of the food items taken by sea otters were bivalves, especially *Saxidomus gigantea* (Calkins 1978). The Alaskan otters "dug out clams with their forepaws while maintaining a head downward position" in intertidal and shallow subtidal water. However, Shimek's (1977) description is the only detailed underwater observation of sea otters foraging on soft substrate. Detailed observations of sea otters taking prey from soft substrates are more difficult than those on rock, because the otter's disturbance of the bottom often results in clouds of sediment obscuring further vision. In the present account, we describe underwater observations of sea otters digging clams in a silty sand substrate and present information about the impact of this foraging on the distribution and abundance of subtidal clams at Monterey Harbor, Calif.

Observations

In 1976-77 we observed sea otters eating large numbers of the Washington clam, *Saxidomus nuttalli*, primarily in two specific areas of Monterey Harbor (A and B of Figure 1). From vantage points along the floating boat slips and elevated wharves, we observed sea otters at the surface feeding on 211 prey items: *S. nuttalli* (88.6%); the crabs *Pugettia producta* (4.2%) and *Cancer* sp. (3.3%—probably *C. antennarius* or *C. productus*, but not *C. magister*); the rock jingle bivalve *Pododesmus cepio* (1.4%); and unidentified items (2.4%). During spring 1976, as many as four sea otters were foraging at one time in the harbor vicinity, but an average of about one sea otter was observed on 38 counting trips made to the area.

The underwater path of foraging sea otters could often be observed from the surface by following the trail of air bubbles escaping from their compressed fur. The paths of foraging dives made in the inner harbor were often contorted, 50-60 m or more long, and lasted 45-80 s. These dives usually produced no prey, but the prey taken were mostly crabs and rarely clams. On those dives that resulted in the capture of kelp crabs, sea otters usually (eight out of nine dives) finished their search with a swim under 10-20 m of the floating docks in the inner area of the harbor. During scuba dives in this area, we repeatedly observed kelp crabs on the undersides of these floats and rarely elsewhere. It was difficult to observe the paths of

[1]Wild, P. W., and J. A. Ames. 1974. A report on the sea otter, *Enhydra lutris* L., in California. Calif. Dep. Fish and Game Mar. Resour. Tech. Rep. 20, 93 p.

[2]Miller, D. J., J. E. Hardwick, and W. A. Dahlstrom. 1975. Pismo clams and sea otters. Calif. Dep. Fish Game Mar. Resour. Tech. Rep. 31, 49 p.

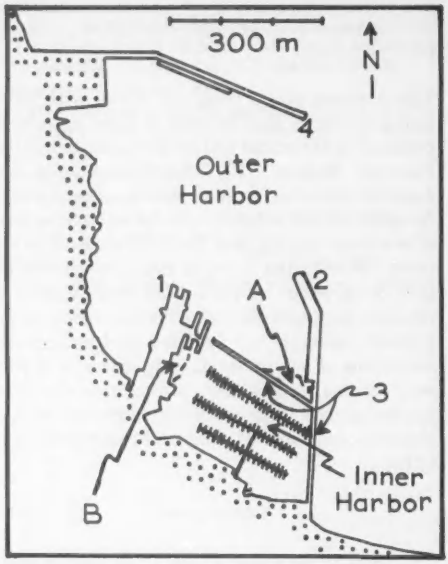

FIGURE 1.—Monterey Harbor, Calif. High densities of clams were foraged by sea otters in areas A and B. 1 = Fisherman's Wharf; 2 = Wharf No. 2; 3 = north and east sea walls of the inner harbor; 4 = breakwater for the outer harbor. (Traced from an aerial photograph in Haderlie and Donat 1978.)

dives made in the middle of the outer harbor, but sea otters usually surfaced without prey 50 m or more from the start of the dive. However, the paths of feeding dives in the two locations where clams were taken in abundance were usually quite short, only 10 m or less.

The usual sequence of dives in the harbor region began with otters making one to three 50-90 s dives that produced no prey. After about 10-20 s on the surface and a little grooming, the otters usually dove again to the same spot. A series of short (25-40 s) dives followed the initial dives, and each of these invariably resulted in a single *S. nuttalli* about 10 cm long. The otters took 30-90 s to open and eat the clams before diving to the same spot. Sometimes they pounded the clams on a rock anvil on their chest; other times they simply twisted or pried the clams open with their teeth. An average of 6 and as many as 19 clams were taken in a single series of these dives. Following such a series, otters usually spent up to 30 min grooming before they swam away, sometimes to forage in a new location.

In spring 1976, we conducted an underwater survey of most of the bottom of the inner and outer harbor, noting variations in the substrate and counting protruding clam siphons in haphazardly tossed ¼ m^2 quadrats. Depths in the harbor ranged from 2 to 8 m, with area A being 4.5 m and area B 2-3 m (Figure 1). The substrate in much of the enclosed inner harbor was black mud and silt, and most of the rest of the harbor (including areas A and B) was silty sand. The two areas where otters fed extensively on clams had high densities of clam siphons: for area A, $\bar{x}$ = 13.5/m^2, SD = 8.9, n = 19; for area B, $\bar{x}$ = 9.3/m^2, SD = 7.2, n = 16. The area under Wharf No. 2 adjacent to area A had even higher densities of siphons: $\bar{x}$ = 17.4/m^2, SD = 11.9, n = 18. However, other areas of the harbor had siphon densities < 1.0/m^2, and the black mud of the inner harbor had densities < 0.04/m^2. We inserted a slender rod down siphon holes in the substrate until the rod contacted the clam shell, and, with considerable difficulty, we used a stream of freshwater from a garden hose to obtain a few 8-14 cm long clams from area A. We used these specimens to distinguish the two species present by the morphology of the protruding siphons. The species composition in areas A, B, and under Wharf No. 2 were the same: 95% were *S. nuttalli*, 5% were the gaper clam, *Tresus nuttallii*. In this way we also determined that the clams were located 10-50 cm into the substrate and that larger individuals of both species tended to occur at the deeper end of this range in the sediment. We recorded the densities of clam siphons in area A and also in the adjacent area of highest density under Wharf No. 2 at approximately bimonthly intervals from February 1976 to March 1977. The densities and proportions of the two species of clams did not change (ANOVA, $P > 0.05$).

The bottom in the two areas where sea otters took large numbers of clams was littered with hundreds of shells, both on the surface and mixed into the sediments. About 58% of the shells did not have pairs of connected valves, and about one-third of the valves were broken. Of 89 shells sampled, 99% were *S. nuttalli* and 1% were *T. nuttallii*. The bottom topography was hummocky in these areas, and there were many craters 0.5-1.0 m across and 10-15 cm deep. The bottom under Wharf No. 2, where the density of clam siphons was highest, was mixed with debris consisting of chunks of asphalt apparently from resurfacing of the road on the wharf and of clumps of large barnacle, *Balanus nubilus*, tests which had fallen

from the massive barnacles encrusting the pilings. There were considerably fewer craters in this area compared with the adjacent area A, and our attempts to dig into the substrate under the wharf proved difficult as a result of the debris embedded in the sediment.

Sea otters were in the process of foraging on clams during several of the scuba dives in area A. Although these otters were not bothered by our presence under water, attempts to observe precisely how they were capturing clams usually failed because they stirred up large clouds of sediment that obscured all of their activity. When the otters stopped foraging and the clouds of sediment dispersed, a large hole up to 1.0-1.5 m across and 0.5 m deep had obviously resulted from their digging. The sides of these holes were initially nearly vertical, but collapsed within minutes.

Details of a sea otter digging for clams were observed by the first author on a single occasion on 30 March 1977, when a strong current rapidly dispersed the clouds of sediment. Upon observing a young male otter begin a typical sequence of foraging dives in area A, the observer moved along the bottom and approached the digging site from an upstream direction. The otter was clearly visible at a distance of 5 m and was just leaving the bottom after completing the second longer dive of the series. He returned to the bottom within 20 s but abandoned the initial digging site, leaving a small hole about 0.5 m across and 25 cm deep. Instead, on this third dive, he moved immediately to a new spot about 4 m away and began to dig rapidly with his front paws in a fashion very much like a dog, producing a large conical cloud of sediment extending downstream. Digging lasted about 45 s, followed by a 20 s surface interval. On the fourth dive the otter resumed digging in the same spot, and as during all digging periods, he faced into the current. The observer was able to approach < 1 m from the sea otter by creeping up in a prone position on the bottom while the otter substantially enlarged the hole to a short trench about 1 m long, 0.5 m across, and 25 cm deep by digging rapidly with both front paws. His back flippers were moving at a slower rate, which probably helped maintain his position and also appeared to assist in digging. Toward the end of the digging on this dive the otter began to roll repeatedly from side to side to enlarge the front end of the trench laterally, until he apparently encountered a clam and suddenly surfaced for 45 s. On the fifth dive this rapid process of rolling and lateral digging with the front paws continued again for about 30 s until another clam was caught and the activity suddenly stopped. The hole at this time was over 0.5 m deep and the otter's body was entirely below the level of the substrate surface while digging. The otter used this process of lateral digging on three more dives lasting about 30 s each with 40-60 s surface intervals, before the observer ran out of air and surfaced. The trench at that time was over 1.5 m long and remained about 0.5 m wide and deep. The otter terminated the series of feeding dives with one additional dive while the observer was at the surface. It paid no apparent attention to the observer's close presence during the entire series. Simultaneous observations by the second author from the surface indicated that none of the first three dives (including two dives at the first spot) produced a clam, but that each of the six subsequent dives resulted in a single clam. The otter did not use a rock to open the clams.

Discussion

In 1966, prior to the return of sea otters to Monterey Harbor, Calif., Department of Fish and Game divers made qualitative surveys of the bottom and used a garden hose to remove several clams from the substrate for identification. The bottom topography was smooth, clams were abundant, and *T. nuttallii* was the dominant species removed from as deep as 50 cm in the substrate (Ebert[3]). Follow-up survey dives soon after the return of sea otters indicated that clams were less abundant and the bottom topography was hummocky (Ebert, see footnote 3). Although definitive quantitative data are not available for that period, and although construction and dredging operations in the inner marina portion of the harbor may have had important impact on clam populations, information in the present report indicates that sea otters may have limited the abundance and distribution of *S. nuttalli* and *T. nuttallii* and that *T. nuttallii* is now only a minor species. The cause of this apparent shift in dominance from *T. nuttallii* to *S. nuttalli* is unclear. Our limited measurements of the depths of these clams in the substrate indicated that larger individuals were found deeper (to about 50 cm), but that neither

[3]E. E. Ebert, Director, Marine Culture Laboratory, California Department of Fish and Game, Granite Canyon, Coast Route, Monterey, CA 93940, pers. commun. June 1979.

species had a depth refuge from predation by sea otters, which excavated deeper than 50 cm. *Tresus nuttallii* attains larger size than *S. nuttalli* (pers. obs.), and if sea otters prefer larger clams, they may have preyed preferentially upon *T. nuttallii*. However, clams remained abundant in small areas of the harbor in spite of heavy predation by sea otters. Densities under Wharf No. 2 averaged about 17 clams/m^2; and in this area they appear to have a partial refuge from sea otters, which may have found it too difficult to dig through the debris of chunks of asphalt and clumps of barnacle tests embedded in the sediment. No such impediment to digging exists in areas A and B, where clams have persisted in somewhat lower densities of about 14 and 9/m^2, respectively. However, the species composition of clams was the same under Wharf No. 2 and in areas A and B, regardless of predation intensity.

By following tagged animals, Loughlin (1977) showed that certain sea otters made daily foraging trips to Monterey Harbor from rafting locations as far as 2 km away. In the present descriptions of their dive paths, sea otters feeding on items other than clams apparently located prey in a random manner similar to Shimek's (1977) description of an otter patting the surface of rocks and feeling the cracks. Observations of the bubble paths of otters taking clams in areas A and B of the harbor, however, indicated that they usually did not spend time searching for a suitable place to dig, nor did visual selection of a patch of clams appear to occur. If the density of clams in area A averaged 14/m^2, and if an average spot dug up by an otter was 0.5 × 1.5 m (0.75 m^2) as observed in this report, then random digging in area A would produce about 10 clams. This is greater than the average number of six clams taken by otters on a series of dives. Perhaps the otters had learned the location of the clam patches, and because sediment clouds normally prevented visual cues as soon as the substrate was disturbed, they simply dug haphazardly within the patch. Indeed, Gentry and Peterson (1967) compared the underwater visual acuity of sea otters with the sea lion, *Zalophus californianus*, and harbor seal, *Phoca vitulina*, and proposed that vision in otters may be better adapted for aerial situations of predator detection rather than for underwater prey location.

The strategy of repeatedly enlarging the hole to capture clams is a good one, because it makes efficient use of the labor to start the hole on initial dives. Anyone who has dug in sand at the seashore knows that it is relatively easy to enlarge a hole, and it would be advantageous to do this rather than dig straight down for each individual clam. The behavior of digging like a dog has also been reported by Shimek (1977) for a sea otter taking subtidal echiuroid worms and is apparently similar to the behavior of sea otters taking clams in shallow subtidal and intertidal waters in Alaska (Calkins 1978). The holes reported by these authors were only half the size of freshly dug holes at Monterey Harbor, however. The first author has observed similar (1.5 m across and 0.5 m deep) holes dug by otters in the sand channels in 12 m of water off kelp forests at Pacific Grove, Calif. In areas such as Prince William Sound and Monterey Harbor, where otters forage heavily on clams, their digging must cause a major disturbance of the infaunal community.

Sea otters have been termed "keystone predators" (Estes and Palmisano 1974; Estes et al. 1978), because they regulate populations of epibenthic invertebrates, perhaps through a process of switching between prey species. At Monterey Harbor there is circumstantial evidence that sea otters have had a major impact on two other prey items. Surveys by the California Department of Fish and Game showed *C. antennarius* and *C. productus* were taken in abundance by fishermen from the Monterey wharves prior to the return of sea otters, but they were rarely taken at Monterey in 1972-74, while still caught in abundance at piers north of the range of sea otters (California Department of Fish and Game[4]). Observations on the scuba dives reported here for 1976-77 confirm that cancer crabs are rare in the harbor. *Mytilus edulis* and *M. californianus* formed dense clumps on wharf pilings prior to the return of sea otters (Haderlie[5]), but mussels are small and uncommon there now (Haderlie and Donat 1978). Curiously, large specimens of *B. nubilus* are still abundant on the pilings and were not taken in appreciable numbers by sea otters, even though these barnacles were taken frequently by otters at other locations in the Monterey area (pers. obs.). The factors which regulate prey selection by sea otters remain poorly understood.

[4]California Department of Fish and Game. 1976. A proposal for sea otter protection and research and request for the return of management to the State of California. Calif. Dep. Fish Game, Oper. Res. Branch, Vol. 1: Text and summaries, 271 p.

[5]E. C. Haderlie, Professor, Naval Postgraduate School, Monterey, CA 93940, pers. commun. May 1976.

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EFFECT OF ZINC ON FIN REGENERATION IN THE MUMMICHOG, *FUNDULUS HETEROCLITUS*, AND ITS INTERACTION WITH METHYLMERCURY

Methylmercury has been found to retard fin regeneration in the marsh killifish, *Fundulus confluentus*, and striped mullet, *Mugil cephalus* (Weis and Weis 1978). In *F. confluentus* the retarding effect of methylmercury was masked in water of reduced salinity (9‰). Cadmium, which also retarded fin regeneration in killifish (Weis and Weis 1976), interacted antagonistically with methylmercury so that fish exposed simultaneously to the two metals exhibited growth rates comparable to controls (Weis and Weis 1978).

This paper reports on the effects of zinc on regeneration in the mummichog, *F. heteroclitus*, and the effects of combinations of methylmercury and zinc on this process.

Methods

Fish were collected by seining in the vicinity of Montauk, N.Y. The lower portion of each caudal fin was amputated with a scalpel, and approximately 15 fish were placed in each of several all-glass aquaria with 10 l of 30‰ salinity water. The temperature was 20°-22° C and the photoperiod was 14 h light/10 h darkness. Fish were fed commerical fish food and live grass shrimp, *Palaemonetes pugio*. Tanks were dosed with methylmercuric chloride (I.C.N. Pharmaceuticals, Plainview, N.Y.[1]) from a 0.1 mg/ml stock solution in 0.2% $NaHCO_3$ to yield a final calculated concentration of 0.050 or 0.025 ppm depending on the experiment, and/or with $ZnCl_2$ (Reagent Grade, Fisher Scientific) from a 1.0 mg/ml stock solution to yield calculated concentrations of 1.0, 3.0, or 10.0 ppm. Aquaria were washed, refilled, and redosed after 2, 4, 7, 9, and 11 days. Regenerating fins were measured with a calibrated ocular micrometer in a stereomicroscope at 7, 9, 11, and 14 days. Experiments were terminated at 2 wk because after that time it became difficult to ascertain the point at which the amputation had been made. The amputation plane can be seen clearly in Figure 1, a control fin 1 wk after amputation.

Three experiments were performed. Experiment I involved exposure of fish 3.5-4.2 cm stan-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

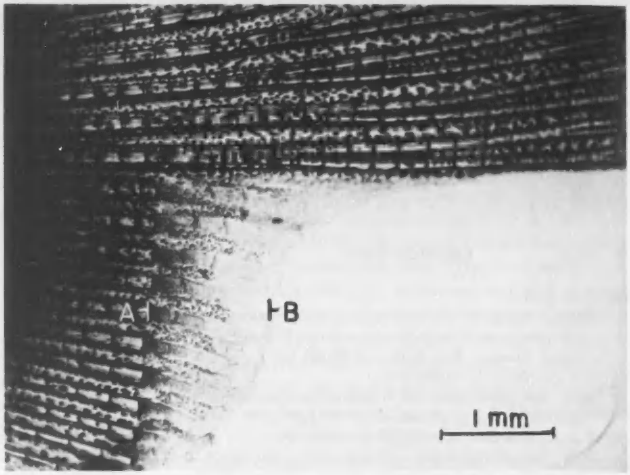

FIGURE 1.—Photograph of regenerating caudal fin, 1 wk after amputation. Measurements were made at A to B.

dard length (SL) to 0.05 ppm methylmercury, 1.0, 3.0, or 10.0 ppm zinc or combinations of 0.05 ppm methylmercury with 1.0, 3.0, or 10.0 ppm zinc. Experiment II was similar, but used 0.025 ppm methylmercury and fish 4.1-5.2 cm SL. Experiment III used 0.05 ppm methylmercury and the same concentrations of zinc, but was performed in water of reduced salinity (10‰) on fish 4.3-5.1 cm SL.

Fish were frozen at the end of some experiments and later analyzed for metal uptake by atomic absorption spectrophotometry (cold vapor technique for mercury, flameless atomic absorption spectrophotometry for zinc). These analyses can be considered accurate within 10%.

Results

In Experiment I, caudal fin regeneration was retarded by methylmercury and was accelerated by zinc in a dose-dependent fashion. The retardation produced by the mercury could be partially counteracted by the zinc (Figure 2). Analysis of variance of day 14 (Table 1) showed significant effects of mercury, and of zinc, but not of interaction.

Experiment II, using 0.025 ppm methylmercury, produced similar results (Table 2). It can be seen that zinc again accelerated growth in a dose-dependent manner and counteracted the methylmercury-caused depression of growth. Only the group in methylmercury alone and the group in 10 ppm zinc were significantly different from controls ($P \leq 0.05$) as determined by the t-test.

TABLE 1.—Analysis of variance on effects of methylmercury and zinc on fin regeneration in *Fundulus heteroclitus*.

Source of variation	df	SS	MS	F	P
Hg	1	24.778	24.778	173.671	0.001
Zn	3	2.200	0.733	5.139	0.003
Hg × Zn	3	0.411	0.137	0.960	0.416

TABLE 2.—Growth of tail regenerates in *Fundulus heteroclitus* exposed to methylmercury and zinc for 14 days in Experiment II and 11 days in Experiment III.

	Experiment II		Experiment III	
Exposure	n	mm ±SE	n	mm ±SE
Controls	12	3.62±0.078	12	2.28±0.069
meHg	15	3.31±0.128*	8	1.67±0.125*
meHg + 1 ppm Zn	12	3.59±0.099	7	1.82±0.094*
meHg + 3 ppm Zn	13	3.49±0.116	2	2.14±0.060
meHg + 10 ppm Zn	12	3.50±0.084	1	2.24±0.00
1 ppm Zn	13	3.73±0.144	11	2.43±0.098
3 ppm Zn	14	3.86±0.142	9	2.44±0.111
10 ppm Zn	10	4.18±0.159*	2	2.46±0.020*

*Significantly different from controls ($P<0.05$) by t-test.

In Experiment III (10‰ salinity) a similar pattern was seen (Table 2). High mortality due to interruption in air supply caused the experiment to be terminated early. The groups in methylmercury, methylmercury + 1 ppm zinc, and in 10 ppm zinc were significantly different from controls, as seen by the t-test.

Analysis of mercury uptake revealed considerable variation (Table 3). However, it seems likely that the tissue residues are dose dependent and that zinc does not change the uptake of mercury

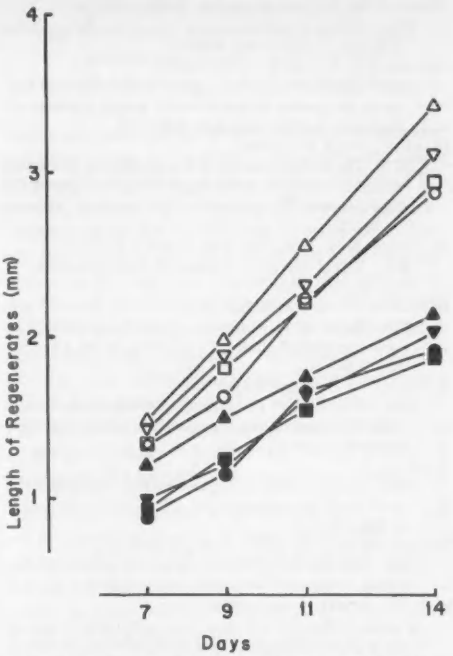

FIGURE 2.—Regenerative growth of tail fin of *Fundulus heteroclitus* exposed to methylmercury and zinc in seawater, Experiment I.
Key: △ 10.0 ppm Zn (n = 15), ▽ 3.0 ppm Zn (n = 15), □ 1.0 ppm Zn (n = 15), ○ Control (n = 14), ▲ 0.05 ppm meHg + 10.0 ppm Zn (n = 11), ▼ 0.05 ppm meHg + 3.0 ppm Zn (n = 12), ■ 0.05 ppm meHg + 1.0 ppm Zn (n = 9), ● 0.05 ppm meHg (n = 12).

TABLE 3.—Average mercury uptake (ppm Hg/wet weight ± SE) by *Fundulus heteroclitus*.

Item	Control Uptake	*n*	Hg Uptake	*n*	Hg + 10 ppm Zn Uptake	*n*
Experiment I:						
Carcass	n.d.[1]	3	32±5.0	3	37±7.2	3
Brain	n.d.	3	11±0.9	3	19±4.8	4
Experiment II:						
Carcass	n.d.	3	7.4±0.7	3	15.4±3.1	5
Brain	n.d.	3	4.8±2.6	3	9.7±1.6	5
Experiment III:						
Carcass	n.d.	3	33±12	3	25±1.4	3
Brain	n.d.	3	28±6.0	3	25±2.5	3

[1]n.d. = not detectable, <0.03 ppm.

into the brain or the rest of the body. Accumulation of zinc was not altered by methylmercury. Animals in 10 ppm Zn accumulated 246±1.41 ppm; those in 10 ppm Zn + 0.05 ppm meHg accumulated 250±3.54 ppm. Those in 1 and 3 ppm Zn accumulated 221±25.2 and 250±4.95 ppm, showing no clear dose-dependent relationship.

Discussion

The data indicate that in *F. heteroclitus*, zinc can accelerate regenerative growth, and, by so doing, can counteract the retarding effects of methylmercury. In this species, the regeneration rate of controls was similar in 30‰ and 10‰ salinity, and the methylmercury retarded growth at both salinities. This is in contrast to *F. confluentus* in which decreased salinities depressed the regeneration rate, thus masking the effects of methylmercury in water of 9‰ salinity (Weis and Weis 1978).

Methylmercury has previously been observed to retard regeneration (Chang et al. 1976; Weis and Weis 1978) and other developmental processes (Chang et al. 1974). Its action as an inhibitor of mitosis (Ramel 1969) could be the cause of these effects on growth processes. As a potent nerve poison it could further inhibit regenerative growth by interfering with the neurotrophic influence necessary for regeneration.

Previous studies on the effects of zinc on growth include the work of Hirsch and Hurley (1978) in which zinc was found to counteract the teratogenic effects of 6-mercaptopurine in the rat. They felt that the drug lowered DNA synthesis and that the zinc counteracted this. Swenerton et al. (1969) correlated zinc deficiency with reduced DNA synthesis in rat embryos, and Falchuck et al. (1975) have associated zinc with promoting cell division in *Euglena gracilis*. Thus, if zinc can promote DNA synthesis and cell division in fish also, that would account for the observed acceleration of regenerative growth. However, previous studies on fish have not indicated such an effect. Crandall and Goodnight (1962) reported that 1.15 ppm zinc retarded the growth of newborn guppies. Rachlin and Perlmutter (1969) found that 18 ppm Zn reduced the mitotic index of cultured rainbow trout, *Salmo gairdneri*, cells, but that 1.8-10.0 ppm had no effect on the mitotic index.

On the other hand, zinc has often been found to counteract toxic effects of other heavy metals. Dixon and Compher (1977) found that zinc could reverse a cadmium-caused inhibition of regeneration in the newt. Zinc has been found to counteract the toxic effects of mercury in rats (Yamane et al. 1977) and to counteract the teratological effects of methylmercury in killifish embryos (Weis et al. in press).

In view of reports of fin rot of unknown etiology in flatfish from polluted environments (Ziskowski

and Murchelano 1975), the retardation of growth by heavy metals may be of significance in inhibiting regeneration of fins eroded by the benthic substrate.

Addendum

It has recently been demonstrated that, in certain poeciliid fishes, some environmental variables which affect general growth rate do not affect the rate of fin regeneration. Factors which do cause differences in length of regenerated fin generally affect the time needed for wound healing and blastema formation, rather than rates of regeneration per se (E. Zimmerer, Ph.D. dissertation, Rutgers University, 1980). We tested the data represented in Figure 1 for this possibility. In regression analysis, the slope equals regenerative rate per se and the elevation (y-intercept) represents the time needed for wound healing and blastema formation. Analysis of covariance indicates that when Hg treated fish are compared with control fish, both the slopes and y-intercepts are significantly different (F = 10.23 and 80.76, respectively). Similarly, when 10 ppm Zn treated and control fish are compared, the slopes and y-intercepts are significantly different (F = 6.83 and 41.29, respectively). Therefore, it appears that these heavy metals affect both the initial wound healing and blastema formation and the rate of regeneration per se.

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SOUTHERN DISTRIBUTION OF THE ATLANTIC WHITESIDED DOLPHIN, *LAGENORHYNCHUS ACUTUS*, IN THE WESTERN NORTH ATLANTIC

Two mass strandings of the Atlantic whitesided dolphin, *Lagenorhynchus acutus*, in New England—Wellfleet, Mass., 11 May 1973 and Edmunds, Maine, 6 September 1974—initiated investigation at the New England Aquarium, Boston, into this species' life history and pathobiology. Previous distribution records for this species in the United States were reported by Cope (1876), True (1885, 1889), and Schevill (1956). Most references define this dolphin's southern distribution as Cape Cod, Mass. We believe this is based on a 206 cm female reported to have been collected near Portland, Maine, and described by Cope (1876) as *L. perspicillatus* (= *L. acutus*). Norton (1930) redescribed the correct collecting site as Cape Cod.

The first confirmed Cape Cod report, although not a stranding, was on 14 September 1954 when a school sighting and harpooned specimen were reported by Schevill (1956). This school, about 12 animals, was located 93 km east of Cape Cod in water 145 m deep (Figure 1, number 3).

The following accounts, arranged in chronological order, update our present knowledge of this species' southernmost known occurrence in the western North Atlantic. Information is based upon stranding records of the Smithsonian Institution and the New England Aquarium, along with an examination of the collections of the American Museum of Natural History, New York, N.Y.; Academy of Natural Sciences, Philadelphia, Pa.; U.S. National Museum, Washington, D.C.; and the Museum of Comparative Zoology, Harvard University, Cambridge, Mass. Paragraph numbers below correspond to locality numbers in Figure 1 and to reported body measurements given in Table 1. Abbreviations for collection numbers are as follows: MCZ = Museum of Comparative Zoology, Harvard University, NEA = New England Aquarium, USNM = U.S. National Museum.

1. One male (USNM 22934) captured by the U.S. Fisheries schooner *Grampus* 20 mi (37 km) south of Montauk, Long Island, N.Y. (lat. 40°38′ N, long. 71°49′ W), 19 May 1888. This specimen was reported to have been captured from a school of about 100 animals.

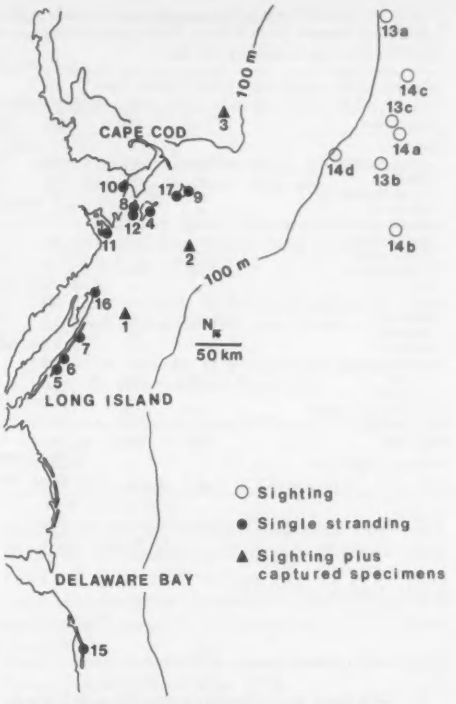

FIGURE 1.—Southernmost east coast locations of known Atlantic whitesided dolphin sightings. Numbers refer to specimens described in Table 1 and in text.

2. One female (USNM 22942), also captured by the *Grampus*, taken south of Cape Cod Islands (lat. 40°43′ N, long. 70°32′ W). No date recorded but because of its proximity to the prior animal's catalog number, we believe this animal was taken on the same cruise.

3. One female (MCZ 48548) harpooned from a small school off Cape Cod (lat. 41°35′ N, long. 68°55′ W), 14 September 1954 (Schevill 1956).

4. One skull (MCZ 48549) collected during the winter 1954-55 at South Beach, Martha's Vineyard, Mass.

5. One specimen washed ashore live at Ocean Beach, Fire Island, Long Island (lat. 40°39′ N, long. 73°09′ W), April 1971. Length estimated at about 7.5 ft (229 cm), sex undetermined. Skull measurements: condylobasal length, 391 mm; rostrum length, 196 mm; tooth width, up to 4 mm; dental formula $\frac{33-}{34-34}$.

TABLE 1.—Selected body measurements, nearest whole centimeter, of *Lagenorhynchus acutus* from the southernmost known occurrences in the western North Atlantic. Data in parentheses converted from English to metric. Doubtful measurements were not included. Localities are given in Figure 1 and text.

Measurement	Locality number and sex								Range	Percentage of total length	
	1(M)	2(F)	3(F)	7(M)	9(F)	10(F)	11(M)	12(-)		Range	Mean
Snout to:											
Notch, total length	(150)	(209)	225	233	165	224	202	(241)	150-241	—	—
Flipper	—	(38)	40	32	18	35	30	(41)	18-41	10.9-18.2	15.4
Tip of dorsal fin	—	—	87	88	93	119	112	—	87-119	37.8-56.4	48.3
Genital slit	—	(137)	—	153	112	157	125	(173)	112-173	61.9-71.8	67.2
Anus	(109)	—	—	—	118	165	141	(182)	109-182	69.8-75.5	72.6
Apex of melon	—	—	4	5	3	5	5	—	3-5	1.8-2.5	2.1
Center of eye	(22)	—	—	28	22	25	24	—	22-28	11.2-14.7	12.6
Angle of mouth	(19)	(25)	—	23	17	21	20	—	17-25	9.4-12.7	10.7
Ear	—	—	—	37	16	33	29	—	16-37	9.7-15.9	13.7
Girth:											
Maximum	—	—	—	103	91	119	121	—	91-121	43.8-59.9	53.0
At axilla	—	—	—	85	84	106	108	—	84-108	42.1-53.5	48.4
At eye	—	—	—	82	68	80	80	—	68-82	35.2-41.2	37.9
Flipper lengths:											
Anterior	(24)	(32)	—	34	25	34	28	(36)	24-36	13.9-15.3	15.0
Posterior	—	—	25	23	16	25	20	(24)	16-25	9.7-11.2	10.3
Maximum flipper width	(8)	(12)	—	14	9	12	11	(13)	8-14	5.3-6.0	5.5
Dorsal fin height	(15)	(22)	24	—	12	25	18	(22)	12-25	7.3-10.7	9.7
Fluke width	(35)	(57)	65	55	36	55	43	—	35-65	21.3-28.9	24.4
Number of visible teeth	—	—	30-30 31-32	30-30 30-30	31-29 32-31	—	30-32 30-30	33-30 32-31	—	—	—

6. One specimen, length and sex unknown, found along Patchogue, Long Island (lat. 40°43′ N, long. 72°57′ W), December 1973. Only the head and the tail were recovered. Estimation of total length from photographs is 160 cm. Tooth count from visible teeth was $\frac{-25}{-31}$.

7. One dead male found in surf line at Village Beach, Village of Westhampton Beach, Long Island (lat. 40°48′ N, long. 72°38′ W), 1 May 1974. Currently, the skeleton is on display at the New York Ocean Science Laboratory, Montauk, Long Island.

8. Decayed carcass of a 150 cm individual (skull USNM 504292), sex indeterminate, was examined on the southeastern corner of Pasque Island, Mass., Nantucket Sound (lat. 41°26′ N, long. 70°51′ W), 5 July 1975. According to residents, this animal had stranded 2 or 3 mo earlier thereby placing the stranding date in April or May.

9. A female (NEA MH7622) found live and later died on the southern side of Nantucket Island, Mass. (lat. 40°14′ N, long. 70°00′ W), 15 February 1976.

10. A female (NEA MH7670), 127.6 kg, stranded alive and later died at Marion, Mass. (lat. 41°42′ N, long. 70°46′ W), 28 April 1976.

11. One dead male (NEA MH7672), 109 kg, found on the eastern edge of Easten's Beach, Newport, R.I. (lat. 41°29′ N, long. 71°17′ W), 1 May 1976.

12. One decayed specimen (NEA MH76129), sex unknown, thought to have stranded during spring 1976. Found early May on the outer side of Cuttyhunk Island, Nantucket Sound, Mass. (lat. 41°25′ N, long. 70°56′ W).

13. Three 1976 sightings reported southeast of Cape Cod along the southeast edge of Georges Bank by the NOAA Ship *Albatross IV*, fall survey 76-09:

a. School of 15-20 animals, lat. 41°13′ N, long. 66°15′ W, 27 March.
b. Two animals, lat. 40°10′ N, long. 67°12′ W, 2 April.
c. Five animals, lat. 40°26′ N, long. 67°03′ W, 2 August.

14. Four sightings on 2 January 1977 during U.S. Coast Guard aerial overflights during the *Argo Merchant* Oil Spill (Grose and Mattson[1]):

a. Two animals, lat. 40°21′ N, long. 66°58′ W.
b. One animal, lat. 39°29′ N, long. 68°20′ W.
c. One animal, lat. 40°34′ N, long. 66°36′ W.
d. One animal, lat. 40°30′ N, long. 68°03′ W.

15. One female, 248 cm, stranded dead about 2.4 km south of the Virginia-Maryland border on Chincoteague National Wildlife Refuge in Virginia (lat. 38°02′ N, long. 75°18′ W), 27 May 1977.

16. A freshly stranded male animal, 234 cm, found at Deerfield Lane Beach, Amagonsett, Long

[1]Grose, P. L., and J. S. Mattson. 1977. The ARGO MERCHANT Oil Spill—A preliminary scientific report. U.S. Department of Commerce, Washington, D.C., Special Report, 323 p.

Island (lat. 41°00′ N, long. 72°05′ W), 30 August 1978.

17. On Nantucket Island, Eel Point (lat. 41°17′ N, long. 70°05′ W), approximately 200 cm specimen (NEA MH78143), sex unknown. The stranding took place on 4 September 1978.

The Virginia stranding extends the southern distribution approximately 700 km southwest of Schevill's (1956) sighting. These reportings south of lat. 41° N indicate that the range of the Atlantic whitesided dolphin is farther south than the Cape Cod area thus extending the range into the Middle Atlantic Bight.

There were two previous published records which had placed this species farther south than Schevill's reporting; however, these appear to be erroneous. True (1885) reported a series of skulls of *L. perspicillatus* (= *L. acutus*) taken in a net fishery at Fort Macon, N.C. That collection of skulls, now in the USNM, were examined and determined to be bottlenosed dolphin, *Tursiops truncatus* (Mead 1975). Rhoads (1903) listed *L. acutus* as possibly occurring off the coast of New Jersey based upon an illustration in Godman (1828). An examination of the original illustration indicates that the species depicted was a common dolphin, *Delphinus delphis*.

These occurrences, as far south as the Chesapeake Bight, indicate the southernmost known extent of the Atlantic whitesided dolphin distribution along the western North Atlantic. It appears from this information that the Atlantic whitesided dolphin has a peak occurrence in the Mid-Atlantic Region during spring and summer.

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ADDITIONAL RECORDS OF THE SCULPIN *PSYCHROLUTES PHRICTUS* IN THE EASTERN BERING SEA AND OFF OREGON

Psychrolutes phrictus Stein and Bond is an unusually large *Psychrolutes* known heretofore from deep water between Monterey, Calif., and northern Oregon. The species can be distinguished from its only congener, *P. paradoxus*, by differences in relative head length, gill raker and pectoral fin ray counts, and the presence of small cirri on both head and body. Recent collections in the Bering Sea and off Oregon supplement the type-description and contribute new information on range and early life history.

During a 2-mo period (summer 1978), while a member of the foreign fisheries observer staff of

the National Marine Fisheries Service, Colin Lau[1] subsampled trawl catches northwest of Unalaska Island on the Japanese fishing vessels *Tomi Maru No. 53* and *Eikyu Maru No. 12*. Lau often noticed a cottidlike fish that he was unable to identify with certainty. Two specimens of this fish, which he preserved, were accessed into the University of Washington fish collection and later identified by the authors as *P. phrictus*. Collection data for the two specimens (UW 20762 and 20763) and for two pelagic juveniles (OSUO 2437 and 2438), obtained in an opening-closing midwater trawl off Oregon (Pearcy et al. 1977), are given in Table 1.

[1]Colin Lau, College of Fisheries, University of Washington, Seattle, WA 98195, pers. commun. October 1978.

Confirmation of the identity of these four specimens was made by comparisons with the meristic and morphometric characters used in the original description (Table 2). Methods for counting and measuring are as in Hubbs and Lagler (1964); measurements were taken to the nearest 0.1 mm with dial calipers; unpaired fin rays and vertebrae were counted on radiographs. These specimens were slightly different from those previously available. The larger specimen from the Bering Sea (UW 20763) has an additional caudal vertebra that may have resulted from development in colder waters. The two juveniles from off Oregon have relatively larger heads than reported previously—evidence of the allometry described by Stein and Bond (1978).

TABLE 1.—Collection data for *Psychrolutes phrictus* in the eastern Bering Sea and off Oregon, 1978.

Specimen source	Date	Position		Haul depth (m)	*Psychrolutes phrictus*		Subsample weight (kg)
		Lat. N	Long. W		Number	Weight (kg)	
Tomi Maru No. 53	19 June	54°31′	167°35′	790	1	—	—
	25 June	54°29′	167°25′	685	1	—	—
	25 June	54°26′	167°30′	740	1	—	—
	26 June	54°41′	167°32′	680	1	—	—
	26 June	54°38′	167°29′	660	[1]1	—	—
	2 July	54°20′	167°22′	900	1	—	—
Eikyu Maru No. 12	13 July	54°22′	166°55′	868	1	5.0	94.7
	20 July	54°18′	167°08′	1,240	1	3.5	118.2
	21 July	54°21′	166°50′	925	1	7.7	135.2
	22 July	54°20′	166°53′	1,050	1	5.4	131.1
	22 July	54°20′	166°51′	940	1	8.0	119.2
	25 July	54°20′	166°52′	850	[2]1	0.3	96.0
	26 July	54°19′	166°52′	925	4	11.4	139.1
	26 July	54°15′	167°07′	1,320	1	4.6	133.3
	28 July	54°22′	166°55′	865	1	7.9	132.2
OSUO[3] 2437	1 Sept.	44°47′	125°50′	495-505	1	—	—
OSUO 2438	2 Sept.	44°37′	125°43′	480-540	1	—	—

[1]University of Washington (UW) collection, Seattle, Wash.; [preserved] specimen UW 20762.
[2][Preserved] specimen UW 20763.
[3]Oregon State University Oceanography (OSUO) collection, Corvallis, Oreg.

TABLE 2.—Meristic and morphometric (measurement in millimeters and percentage within parentheses) characters of *Psychrolutes phrictus* from the eastern Bering Sea and off Oregon.

Item	UW 20762	UW 20763	OSUO 2438	OSUO 2437	Stein and Bond (1978)[1]
Standard length, mm	113	126	28	30	
Fin rays:					
Dorsal	VIII, 20	VIII, 20	VIII, 19 or 20	VIII, 19	VII-IX, 19-20
Anal	13	13	13	13	12-14
Pectoral	23	23	24	23	22-26
Pelvic	I, 3	I, 3	I, 3	I, 3	I, 3
Principal caudal	11	11	11	11	About 13
Gill rakers	11	9	[2]9	[2]9	9-13
Vertebrae:					
Total vertebrae	35	36	34	35	33-35
Precaudal	12	12	13	13	—
Caudal	23	24	21	22	—
Head length[3]	46.4(41)	65.7(52)	15.9(55)	15.3(48)	(43.5-60.6)
Eye length[4]	9.8(21)	9.9(15)	3.2(20)	3.4(22)	(8.6-24.3)
Pectoral fin length[4]	30.2(65)	34.1(52)	7.6(48)	8.0(52)	(44.9-62.3)
Pelvic fin length[4]	10.2(22)	20.3(31)	4.0(25)	4.8(31)	(23.3-34.7)
Preanal length[4]	59.8(129)	75.1(114)	15.4(97)	12.7(83)	(93.8-132.2)

[1]Ranges for data in the original description.
[2]May be incomplete.
[3]Percentage is proportion of standard length.
[4]Percentage is proportion of head length.

Lau's observations on relative abundance of *P. phrictus* indicate that this species may constitute a significant portion of the demersal fish biomass in the area of the Bering Sea where he sampled. During a sampling period from 12 to 31 July, 76 hauls were taken, of which 38 were subsampled. *Psychrolutes phrictus* was present in subsamples from 9 of these 38 hauls and ranked 6 of 44 species found, based on weight. When individuals were present in subsamples of the catch, they represented 0.3-8.2% of the subsample weight (Table 1) and 1.8% of the overall subsample weight for the sampling period. Individuals were also observed casually in hauls where they were not part of the subsample.

The capture of two juveniles off the Oregon coast about 2,500 m above the bottom and about 65 km west of the lower continental slope is evidence that the larvae and juveniles are pelagic. Whether juveniles normally occur so far offshore, and if so, whether such individuals survive to reach the bottom, is not known. *Psychrolutes phrictus* probably leaves the pelagic zone and becomes demersal at about 30 mm. The rationale for this is that the juveniles (28 and 30 mm) reported here were pelagic, whereas those (30 and 49 mm) reported by Stein and Bond (1978) were benthic.

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A RECURRENT MASS STRANDING OF THE FALSE KILLER WHALE, *PSEUDORCA CRASSIDENS*, IN FLORIDA

The false killer whale, *Pseudorca crassidens*, is one of the several species of odontocetes known primarily through its relatively frequent mass strandings. These strandings offer a large amount of natural history data but, in most cases, investigators have been unable, for various reasons, to thoroughly study these events. As a result, very few data are available on the natural history of *P. crassidens* (Mitchell 1975a, b; Purves and Pilleri 1978). *Pseudorca crassidens* is distributed worldwide in temperate and tropical waters (Mitchell 1975b), and frequently strands in large numbers (Norman and Fraser 1948; Dudok van Heel 1962), exceeding 800 in one case (Marelli 1953; Tomilin 1957; Reiger 1975). The series of *P. crassidens* mass strandings we describe herein is the third in Florida in recent years. Caldwell et al. (1970) reported a stranding of 150-175 false killer whales near Ft. Pierce on the Atlantic coast of Florida in January 1970. Little data was collected and most of the animals were apparently buried on the beach. A heretofore unreported stranding occurred on 18-19 July 1972 on the northeast end of Sawyer Key (lat. 24°45.6′ N, long. 81°33.4′ W) in the lower Florida Keys on the Florida Bay (Gulf of Mexico) side. This site is approximately 35 km northeast of Key West (Figure 1). Nineteen animals were involved. Gordon Hubbell[1] estimated the largest animals to be 460 cm (15 ft) long. He measured a 320 cm (10.5 ft) male, a 376 cm (10.3 ft) female, and a 427 cm (14.0 ft) female.

Sequence of Events

1. The Florida Marine Patrol[2] reported a whale stranding near North Captiva Island on the southwest coast of Florida (Figure 1) on the morning of 22 July 1976. We found a dead 440 cm female false killer whale at Redfish Pass (Figure 2) and four live females aground on a sandbar in Pine Island Sound (Figure 2). We necropsied the dead animal on the beach and transported the live animals to Sea World, Orlando, Fla., on 22 July. At least 29 false killer whales had entered Pine Island Sound: 1 died; 4 were stranded alive; 24

[1]Gordon Hubbell, Director, Crandon Park Zoo, Miami, Fla. 33149, pers. commun. 1977.
[2]Florida Marine Patrol, Officer in Charge, Ft. Myers Office, pers. commun. July 1976.

FIGURE 1.—Outline map of south Florida indicating principal stranding sites and possible routes of travel of the false killer whale herd. Fort Pierce is located just north of lat. 27° N on the east coast of the state. Box represents region covered by succeeding figure.

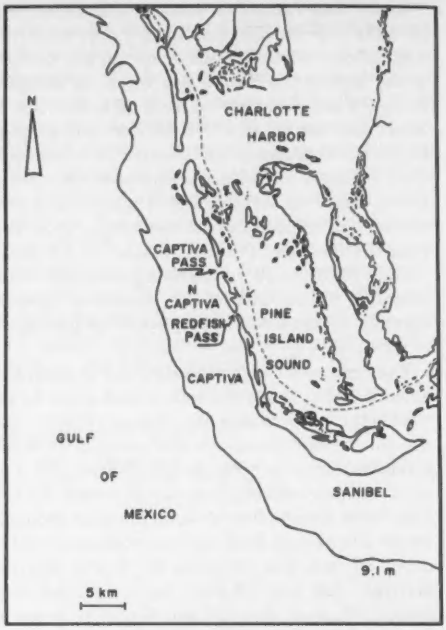

FIGURE 2.—North Captiva Island and vicinity, south Florida, indicating Redfish Pass and Captiva Pass where the false killer whales entered and exited Pine Island Sound. The four females taken to Sea World stranded on a sand bar located off the southeast side of North Captiva (indicated by an arrow). Intracoastal waterway is indicated by dashed line in Charlotte Harbor and Pine Island Sound.

were photographed exiting Captiva Pass (Larson[3]). All moved northward in or near the Intracoastal Waterway after entering Pine Island Sound via Redfish Pass. They continued northward and returned to the Gulf of Mexico via Captiva Pass (Florida Marine Patrol see footnote 2; Larson see footnote 3) (Figure 2). The animals originally entered Redfish Pass at about 0830 h. The tide was rising and near the high point (Florida Marine Patrol see footnote 2). The exact time, and thus tidal conditions when the animals exited Captiva Pass are unknown to us. It is interesting to note that a spinner dolphin, *Stenella longirostris*, herd stranded on Casey Key (lat. 27°12′10″ N, long. 82°30′30″ W) 7 days earlier (Mead et al.[4]). This site is about 75 km north of North Captiva.

2. A herd of 30 false killer whales stranded on Loggerhead Key, Dry Tortugas (Figure 1), at approximately 1300 h on 25 July on a falling tide. This site is some 235 km south of North Captiva Island. The herd was divided into two groups at the time of stranding (Shinn[5]). The animals were pushed back into the water and kept wet by U.S. Coast Guard and National Park Service personnel. We measured and sexed the animals and photographed their dorsal fins and flukes for individual identification of the animals on 26 July. We repeated the measurements and photographs, collected blood samples and marked each animal with a spaghetti tag (Floy Tag FD-68B[6] anchor

[3]Peter Larson, *Sanibel Island Reporter*, Sanibel, Fla., pers. commun. 1976.

[4]Mead, J. G., D. K. Odell, R. S. Wells, and M. Scott. 1978. Biological observations on a mass stranding of spinner dolphins (*Stenella longirostris*) from the west coast of Florida. Unpubl. manuscr. Division of Mammals, Smithsonian Institution, Washington, DC 20560.

[5]Eugene Shinn, U.S. Geological Survey, Miami, Fla., pers. commun. 1976.

[6]Floy Tag & Manufacturing Inc., Seattle, Wash. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tag) on 27 July. A 520 cm male died prior to an attempt to return all of the animals to offshore waters. A group effort by Park Service, Florida Marine Patrol, Coast Guard, and other personnel successfully forced the remaining 29 out to sea. Color photographs and a popular description of this stranding are given by Porter (1977).

3. On 2 August, National Park Service personnel found three shark-eaten *P. crassidens* carcasses floating about 2 km off Cape Sable (Figure 1). They towed these to shore and Odell examined them on 3 August.

4. On 23 August, Odell salvaged 20 *P. crassidens* skulls from carcasses discovered on Cape Sable by the National Park Service on 18 August. The whales were severely decomposed when first discovered and had probably been on the beach for at least 2 wk. Sex determination and external measurements were not possible (Odell and Asper[7]; Odell et al.[8]).

Results and Discussion

We measured 29 of the 30 whales that stranded on Loggerhead Key (total length only). The mean length (±SD) of 12 males was 458±48 cm, range 377-534 cm and 17 females was 416±39 cm, range 328-494 cm. The mean lengths were significantly different at the 0.01 level. The weight-length data (250 kg, 297 cm; 327 kg, 338 cm; 359 kg, 358 cm; 773 kg, 475 cm) from the four live females that we collected at North Captiva Island yielded the following predictive allometric equation corrected for log transformation bias (Beauchamp and Olson 1973): $W = 2.16 \times 10^{-4} L^{2.437}$, where W is weight in kilograms and L is length in centimeters.

The length exponent in the above equation is low when compared with similar equations for several other marine mammals. Bryden (1972) summarized the weight-length relationships for a number of marine mammals. The length exponents for several cetaceans are: *Delphinapterus leucas*—two populations, males, 2.536 and 2.605 (Sergeant and Brodie 1969); *Globicephala melaena*—2.895; *Balaenoptera musculus*—3.25 (Ash 1952); *B. physalus*—2.9 (Ash 1952); *B. borealis*—two populations, 2.43 and 2.74 (Omura 1950; Fujino 1955); and *Megaptera novaeangliae*—3.1 (Ash 1953). The mean (±SD) of these eight length exponents is 2.807±0.283. The relatively low length exponent for *P. crassidens* could be due to the small sample size or perhaps to poor condition of the animals, since we do not know how long the animals had been without food before stranding. However, the 95% confidence limits on the *P. crassidens* length exponent are 2.437±0.564.

The necropsies of six (four captive, two in field) recently decreased whales indicated extensive parasitism. Most apparent in all animals were hundreds (perhaps thousands) of the acanthocephalan worm, *Bolbosoma capitatum*, attached to the walls of the small intestine (Overstreet[9]). We found pieces of intestine with attached acanthocephalans near the Cape Sable animals. Five of the six animals had hundreds of the nematode, *Stenurus globicephalus*, in the pterygoid sinus complex. Three animals had the stomach nematode, *Anisakis* cf. *simplex* (Overstreet see footnote 9). Four animals had *S. globicephalus* in the lungs (Overstreet see footnote 9). Notable was the apparent absence in all six animals of cestode plerocercoid cysts in the blubber. Histopathology revealed that the ultimate cause of death of the four captive females was primarily pneumonia with some parasitic involvement.[10] The pathological condition(s) that led to pneumonia remain speculative. Hall and Schimpff[11, 12] examined the brains of the captive animals and of the male that died on Loggerhead Key and found them free of major neurologic disease, although they stated that some animals exhibited "behavioral symptoms suggestive of

[7]Odell, D., and E. Asper. 1977. A summary of information derived from a mass stranding of *P. crassidens* in Florida, 1976. (Abstr.) Marine Mammal Stranding Workshop, Athens, Ga., 10-12 August, 1977, p. 20-21. U.S. Marine Mammal Commission contract MM7AC020.

[8]Odell, D. K., E. D. Asper, J. Baucom, and L. H. Cornell. 1979. A summary of information derived from the recurrent mass stranding of a herd of false killer whales, *Pseudorca crassidens* (Cetacea: Delphinidae). *In* J. R. Geraci and D. J. St. Aubin (editors), Biology of marine mammals: insights through strandings, p. 207-222. Final Rep., U.S. Marine Mammal Commission contract MM7AC020. Available Natl. Tech. Inf. Serv., Springfield, Va., as PB 293380.

[9]Robin Overstreet, Gulf Coast Research Laboratory, Ocean Springs, MS 39564, pers. commun. September 1976.

[10]Armed Forces Institute of Pathology, Washington, DC 20306, cases 1579706 and 1579707, pers. commun. October 1976.

[11]Hall, N. R., and R. D. Schimpff. 1977. Neuropathology in relation to stranding. 2. Mass stranded whales. (Abstr.) Marine Mammal Stranding Workshop, Athens, Ga., 10-12 August 1977, p. 28-29. U.S. Marine Mammal Commission contract MM7AC020.

[12]Hall, N. R., and R. D. Schimpff. 1979. Neuropathology in relation to strandings: mass strandings. *In* J. R. Geraci and D. J. St. Aubin (editors), Biology of marine mammals: insights through strandings, p. 236-242. Final Rep., U.S. Marine Mammal Commission, contract MM7AC020. Available Natl. Tech. Inf. Serv., Springfield, Va., as PB 293380.

vestibular dysfunction." They also found no parasitic infiltration of the eighth cranial nerves or the vestibular cochlear nuclei.

We examined the reproductive organs from the six fresh carcasses. We judged the male to be sexually mature on the basis of body length (520 cm), total testis weight (8,200 g) and histological demonstration of spermatogenesis. We considered three of the females (body lengths 297, 338, 358 cm) sexually immature. Neither corpora lutea nor corpora albicantia were found in the ovaries (Harrison[13]) and ovary weight was low (13.3, 14.0, and 15.1 g, respectively) compared with the other two females. One female (475 cm) had three corpora albicantia in the left ovary and five to six corpora albicantia in the right ovary (Harrison see footnote 13). Ovary weight was 46.8 g. We also considered the 440 cm female from Redfish Pass to be sexually mature based on ovary weight (65 g) and the presence of three corpora albicantia in the left ovary and six in the right.

Few data are available on sexual maturity and reproduction in *P. crassidens*. Comrie and Adams (1938) examined four 425-450 cm female specimens of *P. crassidens* that were all sexually mature. Norman and Fraser (1948) and Purves and Pilleri (1978) stated that sexual maturity was reached in both sexes at 366-427 cm (12-14 ft) long. Using Norman and Fraser's length range, three females from the Tortugas stranding would be considered immature with the lower limit and nine with the upper limit, and three males would be considered immature with the upper limit.

Hematology

We took blood from vessels in the flukes, flippers, or dorsal fins. Samples for cell counts and hemoglobin determinations were collected in anticoagulant tubes. We collected sera from separate tubes after the blood had clotted, and stored it frozen until it was analyzed. Cell counts were done with a Coulter Model D-2 (Coulter Electronics, Hialeah, Fla.). Serum chemistry analyses were done with a Clinicard Model 368 (Harleco Div. American Hospital Supply Co., Gibbstown, N.J.). This is one of the few (if not the only) times when blood samples have been collected from an entire herd of stranded cetaceans. The data from the 30 Loggerhead Key animals are similar to hematologic values for other small cetaceans (Table 1; Ridgway et al. 1970; Ridgway 1972). Brown et al. (1966) gave some data on blood cell counts from the one false killer whale held at Marineland of the Pacific for 7 yr. Those values are roughly similar to those presented here, but red cell counts were higher ($4.5\text{-}5.2 \times 10^6/mm^3$). The blood values for our four female false killer whales (Table 1) vary somewhat from the Loggerhead Key group and undoubtedly reflect their deteriorating condition. Notable are leucocytosis with an eosinophilia in both groups (Table 1). Serum calcium levels were elevated when compared with other odontocetes. Lactic acid dehydrogenase levels were slightly elevated. All of the above conditions can be indicative of heat stress, parasitism, pneumonia, etc. in other odontocetes, and we assume that *P. crassidens* responds similarly. Alkaline phosphatase levels were low, indicating depletion of reserves. This depletion generally signals impending death in other odontocetes. Blood urea nitrogen and glucose levels were higher in the captives than in the Loggerhead Key animals and could reflect the fact that captives were feeding while the other group had probably not fed for several days. White blood cell counts and lactic acid dehydrogenase levels were the only parameters in which males and females differed significantly (t-test, 0.01 level).

Behavior in Captivity

The four live false killer whales transported to Sea World appeared to adapt to captivity with relative ease. When first put into their pool, they began to swim rapidly around the pool as a group, swimming in a clockwise direction with the largest animal (475 cm), apparently leading the group. They often took food from the hand and were not easily disturbed by routine handling for physical examinations. Within 24 h after their arrival, the largest and the smallest whales were separated from the other two and placed in an adjacent pool. The overall swimming patterns of all the animals remained the same after the separation. However, their swimming pace slowed considerably. The general behavior and apparent rapid adaptation to captivity was quite similar to that observed in a captive false killer whale (animal collected at sea) held at Marineland of the Pacific (Brown et al. 1966).

All of the animals began feeding on mackerel and herring immediately upon arrival. The 338

[13]Richard J. Harrison, Anatomy School, Cambridge University, Cambridge, Engl., pers. commun. 1976.

TABLE 1.—Blood chemistry analyses from two groups of the false killer whale, *Pseudorca crassidens*, stranded in Florida compared with data for the bottlenose dolphin, *Tursiops truncatus*, and the Pacific whitesided dolphin, *Lagenorhynchus obliquidens*.

Parameter	*P. crassidens*[1]			*P. crassidens*[2]			*T. truncatus*[3]		*L. obliquidens*[3]	
	[4]N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	N	$\bar{x}$
Hemoglobin (g/100 ml)	26	15.95	0.84	23	14.27**	1.29	296	14.73*	67	18.61*
Hematocrit (%)	26	46.04	2.05	23	41.26**	3.22	345	44.04*	79	51.67*
Red cell count (10^6/mm^3)	26	4.01	0.27	23	3.80**	0.29	291	4.05*	64	5.56*
Mean corpuscular hemoglobin (pg)	26	39.85	2.04	23	37.53**	2.28	—	[5]36.37	—	[5]33.47
Mean corpuscular volume μ^3	26	115.02	4.61	23	108.70**	6.47	—	[5]108.74	—	[5]92.93
Mean corpuscular hemoglobin conc. (g/dl)	26	34.64	0.95	23	34.56	1.53	—	[5]33.45	—	[5]36.02
White cell count (10^3/mm^3):										
Females	15	7,324*	1,765	23	8,842	3,434	167	9,780*	31	6,668*
Males	11	5,922*	1,203	—	—	—	154	10,675*	41	7,922*
Differential white cell count:										
Bands (immatures) (%)	26	1.31	2.02	23	1.83	2.21	318	1	72	1
Neutrophils (%)	26	73.31	12.43	23	71.83	10.82	318	61	72	42
Lymphocytes (%)	26	13.50	6.59	23	16.96	7.30	318	21	72	29
Eosinophils (%)	26	13.38	9.65	23	9.17	7.65	318	14*	72	22
Monocytes (%)	26	0.58	0.86	23	0.43	0.73	318	3	72	5
Basophils(%)	26	0	0	23	0	0	—	—	—	—
Blood urea nitrogen (mg/100 ml)	29	24.40	4.91	20	46.40**	14.82	232	51*	62	37
Calcium (mg/100 ml)	29	10.67	2.01	17	8.67**	0.56	166	10	29	10
Creatinine phosphokinase (IU/liter)	28	22.93	16.09	13	86.77**	134.82	—	—	—	—
Total cholesterol (mg/100 ml)	29	218.17	47.30	20	305.00**	87.38	301	221	92	154
Lactic acid dehydrogenase (IU/liter)										
Females	17	566.24	80.65	17	364.65**	76.52	100	113	11	179
Males	12	508.83	56.83	—	—	—	80	130	18	244
Alkaline phosphatase (IU/liter)	29	98.72	56.51	20	149.15**	113.80	71	241*	6	256*
Serum glutamic oxaloacetic transaminase (IU/liter)	29	217.52	88.46	20	382.15**	166.82	172	98*	34	110*
Serum glutamic pyruvic transaminase (IU/liter)	29	43.03	63.58	20	31.89**	28.43	88	19	14	45
Glucose (mg/100 ml)	29	80.76	28.76	20	167.10**	52.34	231	129	52	117
Total protein (g/100 ml)	29	7.60	0.56	20	7.32	0.85	133	8.0	10	9.0
Albumin (g/100 ml)	29	3.55	0.34	20	3.71	0.40	109	3.4	10	3.9
Globulin (g/100 ml)	29	3.91	0.73	20	3.55	0.75	—	—	—	—

[1]Animals from Loggerhead Key; each animal sampled once.
[2]The four females held at Sea World; each animal sampled several times.
[3]Data from Ridgway et al. (1970).
[4]Number of determinations made.
[5]Values calculated using mean values for hematocrit, hemoglobin and red cell count.
*Significant difference between males and females, *t*-test, 0.01 level.

cm female consumed an average (±SD) of 20±7.6 kg of mackerel and herring/day, in a ratio of 1.5:1, from 25 July through 9 August. Food consumption decreased significantly on 10 August and the animal died on 13 August. Similarly, the 297 cm female consumed 15.3±4.0 kg of mackerel and herring (2.2:1) between 24 July and 3 August. Food consumption dropped to 1.8 kg on 4 August, rose to 18.6 kg on 8 August when smelt was added to the diet, and then decreased to 5.4 kg on 13 August. Overall food consumption between 24 July and 13 August was 11.7±5.7 kg/day. The animal died on 14 August. The 358 cm female consumed 15.1±8.5 kg of mackerel and herring/day (1.2:1) between 24 July and 7 August. Food consumption decreased on 4 August and remained stable through 7 August ($\bar{x}$ = 9.0±2.5 kg/day). Consumption between 24 July and 3 August was 17.1±8.9 kg/day. Smelt was introduced on 8 August in place of mackerel and total consumption was 22.7 kg. Squid was also added on 9 August. The animal died on 10 August. The 475 cm female had an erratic food consumption (mackerel and herring, 19.4±16.2 kg/day) between 24 July and 29 July when it died. The individual blood chemistry analyses for these four animals reflected their deteriorating condition (Odell et al. see footnote 8) and their combined values were significantly different from the Loggerhead Key animals (Table 1).

Relationships Among Strandings

It is clear, based on photographs, that some of the false killer whales that left Pine Island Sound were the same individuals that stranded on Loggerhead Key. Low altitude (helicopter) aerial photographs were taken of the animals leaving Captiva Pass (Larson see footnote 3). Comparison of these photographs with photographs of dorsal fins of the Tortugas animals provided positive identification of several individuals. Dorsal fin shapes have been used to identify specific individual dolphins over periods of several months

(Würsig and Würsig 1977). Assuming that the animals left Captiva Pass at about 1200 h on July 22, and that they travelled in a straight line, they had to travel about 80 km/day to reach Loggerhead Key at 1300 h on 25 July. When these animals were escorted away from Loggerhead Key on 27 July, they apparently headed northeast (Schimpff[14]). The dead animals we found on Cape Sable were too decomposed to tell if they were the Captiva-Tortugas animals. Three large black whales were seen by a National Park Service pilot several kilometers east of the Dry Tortugas when the other animals were stranded. These may be the first three animals found floating off Cape Sable on 2 August by Park Service personnel, but the evidence is only circumstantial.

The sequence of strandings described herein roughly parallels a series of pilot whale, *Globicephala macrorhynchus*, strandings that occurred in the same vicinity on 19-20 August 1971 (Fehring and Wells 1976). Forty-four pilot whales stranded on Manasota Key and on Gasparilla Island a few kilometers to the south (Figure 1). On 25 August 1971, 12 or 13 pilot whales were found stranded on the Marquesas Keys east of Key West (Figure 1). At least one of these was positively identified to be from the previous stranding.

Fehring and Wells (1976) reported that the pilot whales observed stranding on Gasparilla Island made "a deliberate shoreward movement" as opposed to "disoriented panic." Eugene Shinn (see footnote 5) unknowingly photographed the false killer whales minutes before they beached on Loggerhead Key while taking aerial photographs of the reef formations. The photographs show two close-knit pods of whales heading towards the beach. Fehring and Wells also reported that the behavior of the stranded animals changed after the two largest pilot whales were towed offshore and held there with ropes around their caudal peduncles. The remainder of the animals then showed less tendency to return to shore when pushed off. Several of the larger Loggerhead Key whales were forced offshore (headfirst, without ropes around their tails) in hope that the others would follow. The animals herded offshore returned to the beach when released. The operation was only successful when all of the animals were forced offshore simultaneously and herded to deeper water, using swimmers and two boats. While on the Loggerhead Key beach, the whales were docile, as Fehring and Wells (1976) reported for the pilot whales. Coast Guard personnel who followed the animals offshore reported that the herd split into two groups (one of 17-18 and one of 10 or 11 animals) (Schimpff see footnote 14).

[14]Robert Schimpff, Department of Pathology, College of Medicine, University of Florida, Gainesville, FL 32610, pers. commun. 1977.

Conclusions

From the veterinary medical standpoint, we would doubt the ability of those animals that were necropsied to function normally with the heavy parasite load in the pterygoid sinus complexes. The benefits of forcing live stranded animals back out to sea must be carefully weighed against the benefits of bringing them into captivity, where they can be observed closely and thoroughly necropsied should death occur. If stranded whales are returned to sea, they should be given permanent, individual identification marks (e.g., freeze brands) and, ideally, outfitted for radio tracking.

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OCCURRENCE OF THE FINETOOTH SHARK, *CARCHARHINUS ISODON*, OFF DAUPHIN ISLAND, ALABAMA[1]

Carcharhinus isodon (Valenciennes) is an infrequently encountered species with a poorly known life history. The literature on this species covering the western North Atlantic contains much information on juveniles, but very little on adults. All lengths discussed herein are total lengths.

Radcliffe (1916) reported a single specimen 50.8 cm in the Bureau of Fisheries collection at Beaufort, N.C. Burton's (1940) record of an immature male, 74.4 cm, was the first from South Carolina waters. Specimens examined by Bigelow and Schroeder (1948:304-308) ranged from 46 to 56.7 cm. Springer (1950) examined 20 adult females 147-155 cm collected in December off Salerno, Fla. Thirteen had from one to six embryos 43-48 cm; the remaining seven had enlarged flaccid uteri and medium-sized ovarian

[1]Contribution No. 028, Dauphin Island Sea Lab.

eggs. He suggested a winter pupping period. Clark and von Schmidt (1965) recorded only a single female (76 cm) in 9 yr of shark research off Sarasota, Fla. Dahlberg and Heard (1969) reported the capture of 30 individuals from July through September 1968 off Georgia. Of these, 29 were between 52 and 94 cm. The other specimen (144 cm) was probably the only mature individual, although there was no mention of sex or reproductive development. Hoese and Moore (1977, appendix 5) listed *C. isodon* as a spring through fall spawner based on collections of juveniles at Port Aransas, Texas. Compagno (1978), in his review of the species, assigned this species to the genus *Carcharhinus*.

During longlining operations in the northern Gulf of Mexico in summer 1978, a gravid female and two males were collected off Dauphin Island, Ala. On 2 July 1979 one male and one female were collected in the mouth of Mobile Bay. With so few reports of mature *C. isodon*, these captures will serve to better define the reproductive life history of this species.

On 5 June 1978 the gravid female (139 cm) was collected by longline in water about 5 m deep, approximately 1 km southwest of Sand Island, a small barrier island approximately 5 km south of the east end of Dauphin Island. The shark carried four embryos ranging from 49 to 51 cm. These appeared to be near-term pups. There were two pups in each uterus, each positioned with the head toward the anterior end of the uterus. Each pup was enveloped by a membrane which was filled anteriorly with a translucent yellow fluid. Each had a highly vascularized placenta attached to the posterior portion of the uterus, and the connecting umbilical cords measured 20.6-30.0 cm. Where an umbilical cord attached to a placenta there were three saclike extensions containing a small amount of clear fluid. In earlier embryonic stages of other species of carcharhinid sharks these sacs contain the remaining unconsumed portion of the yolk (Gilbert and Schlernitzauer 1966). The left uterus contained two males; the right uterus one male and one female. The pups and jaws of the female were deposited in the

TABLE 1.—Measurements (centimeters; methods after Bass et al. 1973) of the gravid female *Carcharhinus isodon* and the four pups.

Item	Gravid female	Pup no. 1 male	Pup no. 2 male	Pup no. 3 male	Pup no.4 female
Total length	139	49	51	50.5	50.5
Fork length	118	38.5	40.5	40	40.5
Standard length	106	35	37	36	36.5
Snout to:					
Dorsal 1	46	15.7	16.5	16.5	16.5
Dorsal 2	90	30.2	31.5	31	32.5
Pectoral fin	31.5	11	12.2	11.9	12.2
Pelvic fin	74	22.8	25.4	23.8	24.2
Anal fin	88	28.9	31.9	31.3	30.4
Mouth	9	3.9	3.9	3.8	3.8
Mouth breadth	13	4.1	4.4	4.2	4.1
Between nostrils	7	2.7	2.7	2.7	2.8
Eye diameter	1.8	.8	.8	.8	.7
Gill lengths:					
No. 1	8	2.5	2.3	2.2	2.3
No. 2	8.6	2.6	2.5	2.4	2.5
No. 3	9	2.7	2.7	2.6	2.6
No. 4	8.5	2.5	2.4	2.3	2.4
No. 5	7.5	2.1	1.8	1.8	1.8
Dorsal 1 height	14.7	3.9	3.8	3.5	3.8
Dorsal 1 base	14	4.3	4.6	4.6	5.1
Dorsal 1 free margin	5.5	2.0	2.2	1.8	2.0
Dorsal 2 height	4.0	1.2	1.4	1.4	1.1
Dorsal 2 base	6.5	1.9	2.2	2.2	2.1
Dorsal 2 free margin	5.5	2.0	2.2	1.9	1.9
Anal height	4.3	1.4	1.5	1.5	1.3
Anal base	7.4	2.2	2.4	2.4	2.1
Anal free margin	4.8	1.9	1.9	1.8	1.8
Pectoral height	22	6.0	6.9	6.3	6.5
Pectoral base	8	2.5	2.6	2.5	2.5
Pectoral free margin	6.5	2.2	2.4	2.4	2.4
Pelvic anterior margin	6.5	2.4	2.6	2.7	2.8
Pelvic distal margin	8.8	2.8	2.9	2.7	2.8
Uppper caudal length	39	13.8	14.9	14.7	14.1
Lower caudal length	17.5	5.1	5.5	5.1	5.4
Interspace base dorsal 1 to origin dorsal 2	33	10.1	10.2	9.9	10.3
Interspace base dorsal 2 to caudal pit	10.5	3.8	3.9	3.4	3.4
Origin of pectoral to origin of pelvic	42	11.8	13.2	11.9	12.0
Origin of pelvic to origin of anal	16	6.1	6.5	7.5	6.2
Weight (g)	—	704	810	737	758

University of South Alabama Ichthyological Collection (USAIC 6278). Measurements and weights are found in Table 1.

Since most records of *C. isodon* are of juveniles, there is little information on the reproductive biology of the species. Based on the cited literature and these data, pups appear to be 45-55 cm at birth. However, seasonality is uncertain as the records of Springer (1950) are not in accord with those of either Hoese and Moore (1977) or this report.

Length at maturity can be closely estimated. One male (112 cm) collected 13 July 1978 was immature—based on incomplete calcification of the claspers and incompletely developed siphon sacs, each sac being 7.5 cm long and 1.0 cm wide. The other two males (120 and 127 cm) collected 2 July 1979 and 28 June 1978 had well-calcified claspers and fully developed siphon sacs. The only literature on mature males (Springer 1950) listed lengths of 140-152 cm. Males apparently mature between 115 and 120 cm. Maturity in females must be reached at a larger size. The female collected in July 1979 was 127 cm, yet was immature with only small undeveloped ovarian eggs. The gravid female reported here was 139 cm, and those reported by Springer (1950) were 147-155 cm.

Carcharhinus isodon was only collected when similarly sized specimens of blacktip shark, *C. limbatus*, were caught: 3 *C. limbatus* (126-166 cm) with the gravid female, 12 *C. limbatus* (102-117 cm) with the 112 cm male, 2 *C. limbatus* (111 and 124 cm) with the 127 cm male, and 12 *C. limbatus* (100-130 cm) with the two specimens caught in 1979. If *C. isodon* is an uncommon straggler into the northern Gulf of Mexico it may be schooling with other sharks of like size. Sharks that school have been noted to do so by sex or size (Ford 1921).

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SHEDDING RATES OF PLASTIC AND METAL DART TAGS FROM ATLANTIC BLUEFIN TUNA, *THUNNUS THYNNUS*[1]

In 1971, the International Commission for the Conservation of Atlantic Tunas (ICCAT) recommended that a double-tagging experiment be conducted on Atlantic bluefin tuna, *Thunnus thynnus*, to determine whether plastic or metal dart tags were more efficient and to estimate immediate and instantaneous tag shedding rates. A knowledge of shedding rates is necessary so that appropriate adjustments can be made when estimating mortality rates from tag return data. This study was begun in 1971 by the National Marine Fisheries Service (NMFS), the Woods Hole Oceanographic Institution (WHOI), and the Fisheries Research Board of Canada (FRBC). The

[1]Southeast Fisheries Center Contribution Number 80-14M.

results obtained through 1972, for 580 double-tagged bluefin tuna released during 1971 off the east coast of the United States, were reported by Lenarz et al. (1973). Their results were partially based on tags supplied by the FRBC, some of which had longer streamers than the tags supplied by WHOI. For our present analysis, we used only data from the WHOI tags.

In this paper we present the overall findings obtained through 1978 for 3,121 double-tagged bluefin tuna. These fish were released primarily from U.S. purse seine vessels fishing off the east coast of the United States from Virginia to Massachusetts from 1971 through 1977.

Methods

The U.S. double-tagging program for Atlantic bluefin tuna was conducted jointly by the NMFS and WHOI. Tags and tagging procedures were those described by the Food and Agriculture Organization (1972). All fish were tagged and released from U.S. purse seine vessels (98% of all releases) and from a few sport fishing vessels. Tagging occurred throughout the purse seine fishing season during 1971, 1973, and 1974, and at the end of the season during 1972, 1975, 1976, and 1977. The double-tagging operation was conducted entirely by John Mason during each year except 1974, when two assistants aided in the double tagging. Precise release dates were available for all of the fish. In a few instances only the month and year were known for the recapture data. In these cases, the 15th of the month was arbitrarily selected to represent the recapture date. The vast majority of returns fall into an annual cycle during which the recapture periods are approximately 2-3 summer months. The interval midpoints of the time intervals can be considered to be on a yearly cycle. Therefore, we grouped returns into "first year returns," "second year returns," etc., and calculated average days out from the individual days out for each return. Tag shedding rates were estimated using the notation and methodology of Bayliff and Mobrand (1972) for yellowfin tuna, which Lenarz et al. (1973) used for bluefin tuna and Laurs et al. (1976) used for North Pacific albacore. Chapman et al. (1965) developed the original model with the assumption of only one type of shedding which occurs at a constant instantaneous rate. Bayliff and Mobrand (1972) assumed that there are two types, Type I which occurs immediately after the fish are released and Type II, the type described by Chapman et al. (1965).

Bayliff and Mobrand's modifications[2] of the Chapman et al. (1965) approximate equations for tag returns of double-tagged fish are:

$$n_{ddk} = F\tau N_D\, \pi\rho^2 \exp-(F+X+2L)t_k \qquad (1)$$

$$n_{dsk} = 2F\tau N_D\, \pi\rho(1-\rho\exp(-Lt_k))\exp(-(F+X+L)t_k) \qquad (2)$$

where n_{ddk} = number of returns of double-tagged fish retaining both tags caught during the recapture period t_k,

n_{dsk} = number of returns of double-tagged fish retaining only one tag caught during the period t_k,

F = instantaneous rate of fishing mortality,

N_D = number of double-tagged fish released,

π = proportion of tagged fish which remain alive after the Type-I mortality (immediate) has taken place,

ρ = proportion of the tags which are retained after Type-I shedding (immediate) has taken place,

X = instantaneous rate of mortality due to natural causes, Type-II tagging mortality (long term), and emigration from the fishing grounds,

L = instantaneous rate of tag shedding (Type II), and

t_k = time at the middle of the kth recapture period of length τ ($k = 1, 2, 3$).

From Equations (1) and (2) it follows that

$$\frac{n_{dsk}}{n_{ddk}} = \frac{2(1-\rho\exp(-Lt_k))\exp(Lt_k)}{\rho}$$

and therefore

$$\frac{n_{dsk}}{2n_{ddk}} = \frac{\exp(Lt_k)-\rho}{\rho} = \frac{\exp(Lt_k)}{\rho} - \frac{2n_{ddk}}{2n_{ddk}}.$$

Rearranging terms yields

[2] As pointed out by Laurs et al. (1976), there was typographical error in both Bayliff and Mobrand (1972) and Lenarz et al. (1973) in Equation (2).

$$\frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = \rho\exp(-Lt_k)$$

and hence $$\ln\frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = \ln\rho - Lt_k = Y_k$$

where Y_k is an estimate of the natural logarithm of the proportion of tags retained up to time t_k. Given n_{ddk}, n_{dsk}, and t_k, then L and ρ can be estimated using linear regression. We first estimated these parameters using the usual least-squares linear regression which assumes homoscedasticity. We also believed that it would be appropriate to consider that variability may increase as a function of time as the number of recoveries decreases. To accomplish this, a weighting factor was introduced and a weighted least-squares linear regression model was fitted to calculate values of $\ln\hat{\rho}$ and $\hat{L}$, as was done by Bayliff and Mobrand (1972). The weights for each time interval k ($k = 1, 2, 3$) were equated to the ratio of the number of returns of double-tagged fish during interval k to the total number of returns of double-tagged fish during all k-periods. This can be simply expressed as:

$$\omega_k = \frac{n_{ddk} + n_{dsk}}{\sum_{i=1}^{3}(n_{ddi} + n_{dsi})}.$$

While we consider this a reasonable first approximation of the correct weight, further investigations of the statistical properties of Y_k to formally determine the correct weighting procedure are desirable. Estimates of $\ln\rho$ and L were then made using weighted linear regression.

Results and Discussion

The double-tag releases during 1971 through 1977 and returns in 1971 through 1978 are shown by tag type (Table 1). A sufficient number of tag returns existed to allow examination of three separate recapture periods. Only a few returns existed from beyond the third recapture period. There were approximately equal numbers of each tag type released each year. Table 1 constitutes the basic data used throughout this study. Using the basic data, we estimated values of immediate (Type I) and instantaneous (Type II) shedding rates for each tag type. Further, we tested several hypotheses including: 1) equality of return rates for same year recaptures; 2) equality of return rates by estimated age; and 3) differences in returns and nonreturns over 2 or 3 yr time periods for various time intervals.

Using the double-tagging release data for all years combined (1971-77) the return rate for plastic tags was 5.1% the first year, 8.6% the second year, and 1.6% the third year. The return rate for metal dart tags was 5.5% the first year, 9.1% the second year, and 2.9% the third year. Therefore, for both types of tags the return rates increased the second year and decreased the third year. This should be expected since tagging occurred at the end of the purse seine season for several of the release years studied. Chi-square tests (not cor-

TABLE 1.—Tag releases and returns from northwestern Atlantic bluefin tuna double-tag study. For each of $k = 1$, 2, or 3 recapture periods the number of returns of double-tagged fish retaining both tags is n_{ddk} and those retaining only one tags is n_{dsk}. The average number of days-at-large for each period is t_k.

Tag type	Double-tagged releases		First-year returns			Second-year returns			Third-year returns		
	Year	Number	n_{dd1}	n_{ds1}	t_1 (days)	n_{dd2}	n_{ds2}	t_2 (days)	n_{dd3}	n_{ds3}	t_3 (days)
Plastic dart (D-tag)	1971	150	4	0	7.25	20	9	349.07	3	1	724.00
	1972	75	6	0	12.83	17	4	340.52	1	1	726.50
	1973	134	18	2	18.45	6	4	354.20	0	1	708.00
	1974	629	25	4	12.07	18	12	352.17	4	7	727.82
	1975	50	0	1	40.00	1	1	384.50	0	0	0
	1976	267	12	2	16.36	2	2	341.00	1	2	707.33
	1977	223	3	1	47.50	25	4	361.83	—	—	—
	Total	1,528	68	10	16.46	89	36	352.06	9	12	723.10
Metal dart (H-tag)	1971	162	4	1	18.60	10	9	358.63	2	3	724.80
	1972	77	0	1	11.00	9	11	343.55	0	1	740.00
	1973	131	12	5	16.88	1	3	373.25	0	2	720.00
	1974	666	28	2	10.97	40	13	358.57	15	11	703.19
	1975	58	1	0	43.00	4	5	339.11	2	0	687.50
	1976	271	23	3	23.08	6	0	311.00	0	4	759.25
	1977	228	8	0	36.00	24	2	365.19	—	—	—
	Total	1,593	76	12	18.76	94	43	354.71	19	21	712.48
	Grand total	3,121	144	22	17.68	183	79	353.44	28	33	716.13

rected for continuity) showed that there were no significant differences at the 0.01 level, with 1 degree of freedom, in return and nonreturn rates between tag types for fish at liberty for 1, 2, or 3 yr (Table 2). However, returns were significantly better at the 0.05 level for metal tags in the third year. Further, there was no significant difference at the 0.01 level in the first-year return and nonreturn rates between the two types of dart tag, whether comparing each year individually or comparing all years combined (Table 3).

We also tested for differences in return and nonreturn rates between age-groups. Fish were aged from unpublished length-age tables (Rivas[3]). Chi-square values for fish tagged at ages 1, 2, 3, and 4+, were not significant at the 0.01 level (Table 4). The results of the chi-square test indicated that tag types and ages could be combined.

Unweighted and weighted linear regression models were used to estimate immediate tag shedding rate $(1 - \rho)$ and instantaneous shedding rate (L) (Table 5). The unweighted model for both tags combined yielded an estimate of immediate tag shedding $(1 - \rho)$ to be 0.040 (0.042 for the weighted model). The overall estimate of the instantaneous rate of tag shedding (L) on an annual basis using the model was 0.205 (0.186 for the weighted model). (The annual rate analog for L from the unweighted model is 0.19.) Therefore, the results from each model were similar. We chose to use the unweighted results, which give a slightly higher L value. While results of the chi-square test indicated that tag types could be combined, estimates were also made for each tag type separately to

[3]L. R. Rivas, Southeast Fisheries Center Miami Laboratory, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

TABLE 2.—Chi-square tests (df = 1) of equality of yearly return and nonreturn rates between double-tagged releases for 1971-77 combined, for $k = 1, 2,$ or 3 yr at liberty, using plastic or metal dart tags on bluefin tuna in the northwestern Atlantic Ocean. The number of returns of double-tagged fish retaining both tags is n_{ddk} and those retaining only one tag is n_{dsk}.

	Plastic dart tags			Metal dart tags			
Return year (k)	Double-tagged releases	Total returns kth year ($n_{ddk} + n_{dsk}$)	Return rate	Double-tagged releases	Total returns kth year ($n_{ddk} + n_{dsk}$)	Return rate	Chi-square value
1	1,528	78	0.05105	1,593	88	0.05524	0.272
2	1,450	125	0.08621	1,505	137	0.09103	0.213
3	1,325	21	0.01585	1,368	40	0.02924	5.452*
		Average	0.05104			0.05850	

*$P \leq 0.05$.

TABLE 3.—Chi-square tests (df = 1) of equality of return and nonreturn rates between double-tagged releases recaptured the same year using plastic or metal dart tags on bluefin tuna in the northwestern Atlantic Ocean. The number of returns of double-tagged fish retaining both tags during the first year after release is n_{dd1}, and those retaining only one tag is n_{ds1}.

	Plastic dart tags			Metal dart tags			
Year	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Chi-square value
1971	150	4	0.02667	162	5	0.03086	0.049
1972	75	6	0.08000	77	1	0.01299	3.884*
1973	134	20	0.14925	131	17	0.12977	0.209
1974	629	29	0.04610	666	30	0.04505	0.008
1975	50	1	0.02000	58	1	0.01724	0.011
1976	267	14	0.05243	271	26	0.09594	3.699
1977	223	4	0.01794	226	8	0.03509	1.280
Total	1,528	78	0.05105	1,593	88	0.05524	0.272

*$P \leq 0.05$

TABLE 4.—Chi-square tests (df = 1) of equality of return and nonreturn rates by estimated age between double-tagged releases for all years 1971-77 combined, recaptured the same year, using plastic or metal dart tags on bluefin tuna in the northwestern Atlantic Ocean. The number of returns of double-tagged fish retaining both tags during the first year after release is n_{dd1} and those retaining only one tag is n_{ds1}.

	Plastic dart tags			Metal dart tags			
Estimated age at release	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Chi-square value[1]
1	641	29	0.04524	647	31	0.04791	0.052
2	631	43	0.06815	656	43	0.06555	0.035
3	212	4	0.01887	226	12	0.05310	3.642
4+	44	2	0.04545	64	2	0.03125	0.148
	1,528	78		1,593	88		

[1]No values significant at $P \leq 0.05$.

TABLE 5.—Estimates of immediate $(1 - \hat{\rho})$ and annual instantaneous $(\hat{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for all years combined (1971-77) based on a 3-yr return period using unweighted and weighted linear regression models. (The weights used in the weighted model were equated to the ratio of the number of returns of double-tagged fish during each return period to the total number of returns of double-tagged fish during all periods.)

Model and tag type	$1 - \hat{\rho}$	$\hat{L}$ (annual)
Linear regression:		
Plastic dart	0.027	0.22886
Metal dart	0.049	0.19201
Combined	0.040	0.20452
Weighted linear regression:		
Plastic dart	0.033	0.19200
Metal dart	0.049	0.18213
Combined	0.042	0.18596

indicate the magnitude of the variances of the estimates.

Our estimate of $(1 - \rho)$ is slightly greater than the overall estimate of 0.027 given for bluefin tuna from the northwest Atlantic by Lenarz et al. (1973). The difference is small relative to the precision of the estimates. Our estimate of $(1 - \rho)$ for northwest Atlantic bluefin tuna is less than the value of 0.10 reported for Pacific yellowfin tuna by Bayliff and Mobrand (1972) and the value of 0.12 reported for North Pacific albacore by Laurs et al. (1976).

Our estimate of L is less than the overall estimate of 0.31 reported by Lenarz et al. (1973) for bluefin tuna and the L estimate of 0.278 reported for yellowfin tuna by Bayliff and Mobrand (1972). Our L estimate is greater than the estimates of between 0.086 and 0.098 reported for albacore by Laurs et al. (1976).

As previously noted, there was no significant difference in return rates found for the two types of dart tags for 1971-77. However, from examination of the data presented in Table 1, there appeared to be changes occurring in the shedding rates of each type of tag and a difference between the 1971-73 and 1974-77 time intervals. Therefore, we calculated $(1 - \hat{\rho})$ and $\hat{L}$ for each time interval and conducted chi-square tests (df = 6) for differences in returns over three recapture periods ($k = 3$) between time intervals and between tag types (Table 6). We found significant differences between time intervals for each of the tag types and significant differences between tag types for each of the time intervals. The plastic dart tags became less efficient, i.e., $\hat{L}$ increased over the time intervals, and the metal dart tags improved, i.e., $\hat{L}$ decreased over the time intervals.

The model of Chapman et al. (1965), which was modified by Bayliff and Mobrand (1972), assumes constant L over recapture periods. We decided to examine values of L over the two pairs of recapture periods $k = (1, 2)$ and $k = (2, 3)$ to determine how well our data fit the model. Since only two recapture periods were used, L and $(1 - \rho)$ were estimated by solving two simultaneous equations.

For the tag types and time intervals examined, there is an indication that $\hat{L}$ is not constant (Table 7). In fact, $\hat{L}$ increased in three out of four cases. The sequence of events could have happened due to chance alone, for if the changes in $\hat{L}$ came from a binomial distribution with $P = 0.5$, then the probability of $\hat{L}$ decreasing in three of the four cases or $\hat{L}$ increasing in three of the four cases is ≤ 0.25. However, $\hat{L}$ during the second time period is more than 60% $> \hat{L}$ in the first time period in three cases and only 16% $< \hat{L}$ in the first time period in the other case. While the data do not provide conclusive evidence that L is not constant, it would be dangerous to extrapolate beyond the time period used for analysis.

We previously noted that the 1974 releases were

TABLE 6.—Estimates of immediate $(1 - \hat{\rho})$ and annual instantaneous $(\hat{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for time intervals 1971-73 and 1974-77 based on a $k = 3$-yr return period. (A contingency table, 7×2, was constructed containing the number of double and single returns for each of the three recapture periods plus the number of nonreturns for each tag type and each time interval.) Results of chi-square tests (df = 6) for differences in double and single tag returns and total nonreturns between time intervals and tag types over a 3-yr recapture period are given.

Tag type and time interval	$1 - \hat{\rho}$	$\hat{L}$ (annual)	Chi-square value
Plastic dart:			
1971-73	0.029	0.14838	64.286**
1974-77	0.023	0.28455	
Metal dart:			
1971-73	0.140	0.37163	33.489**
1974-77	0.007	0.17242	
1971-73:			
Plastic dart	0.029	0.14838	18.924**
Metal dart	0.140	0.37163	
1974-77:			
Plastic dart	0.023	0.28455	18.135**
Metal dart	0.007	0.17242	

**$P \leq 0.01$.

TABLE 7.—Estimates of annual instantaneous $(\hat{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for 1971-73 and 1974-77 based on return periods of $k = (1, 2)$ and $k = (2, 3)$.

Tag type and time interval	Return period k	$\hat{L}$ (annual)
Plastic 1971-73	1, 2	0.16017
	2, 3	0.13421
Plastic 1974-77	1, 2	0.09925
	2, 3	0.45207
Metal 1971-73	1, 2	0.27858
	2, 3	0.45271
Metal 1974-77	1, 2	0.09331
	2, 3	0.24632

unique in that three individuals conducted the tagging operation, whereas only one individual tagged and released the remainder of the fish from the other years. Therefore, we analyzed the data from the time intervals 1971-73 and 1975-77 separately from the 1974 data. For the following reasons we decided to examine only two recapture periods, $k = (1, 2)$: 1) 1977 has only two recapture periods possible (Table 1); 2) the number of single as well as double returns for $k = 3$ for both 1971-73 and 1975-77 constitutes very small sample sizes (Table 1); and 3) L appears to have been changing over $k = (1, 2)$ to $k = (2, 3)$ (Table 7).

Our analysis showed (Table 8) that there was a significant difference in return and nonreturn rates between time intervals for each type of dart tag. Also a significant difference in shedding rates was found between the plastic and metal type tags during the time interval 1971-73. A small sample size may account for the lack of a significant difference in shedding rates for each type of tag during the time interval of 1975-77. There also was no significant difference found in the shedding rates between each tag type during 1974. As previously mentioned, fish were released under different circumstances during 1974. During the 1971-73 time interval, plastic tags were found to be superior. We again found that the metal tag improved (Table 8), i.e., $\hat{L}$ decreased, between 1971-73 and 1975-77.

TABLE 8.—Estimates of immediate ($1 - \hat{\rho}$) and annual instantaneous ($\hat{L}$) tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for 1971-73, 1974, and 1975-77 based on a $k = 2$-yr return period. (A contingency table, 7×2, was constructed containing the number of double and single returns for each of the three recapture periods plus the number of nonreturns for each tag type and each time interval.) Results of chi-square tests (df = 4) for differences in double and single tag returns and total nonreturns between time intervals and tag types over a 2-yr recapture period are given. (Results for the period 1971-72 from Lenarz et al. (1973) are shown for comparison.)

Tag type and time interval	$1 - \hat{\rho}$	$\hat{L}$	Chi-square value
Plastic dart:			
1971-73	0.028	0.16017	39.460**
1975-77	0.118	<0.	
Metal dart:			
1971-73	0.169	0.27858	22.186**
1975-77	0.114	0.05860	
1971-73:			
Plastic dart	0.028	0.16017	17.323**
Metal dart	0.169	0.27858	
1974:			
Plastic dart	0.067	0.22615	8.318
Metal dart	0.031	0.12126	
1975-77:			
Plastic dart	0.118	<0.	6.636
Metal dart	0.114	0.05860	
1971-72:			
Plastic dart	0.000	0.21615	
Metal dart	0.099	0.26278	

**$P \leq 0.01$.

Also, $\hat{L}$-values for the plastic tag decreased, but results yielded a negative value for the 1975-77 time interval, which is theoretically impossible and is due to variability in the data.

From our analysis, we cannot conclusively show that one of the two types of dart tags is better for bluefin tuna tagging. Both tag types appeared to improve between 1971-73 and 1975-77. Plastic tags were significantly better than metal in the first period and nonsignificantly better in the second.

We have shown that tag shedding rates vary from 1 yr to another. There are some possible reasons for the observed variability. One reason may be changes in tag design or quality. To our knowledge there was no intentional effort made by the manufacturers to change the design of the metal or plastic dart tags used in this study. A different type of glue, however, was used during 1972 through 1977 for the plastic dart tags. Before using the plastic dart tags, we tested them by pulling on the barb. On several occasions, we discovered that the barbs were not adequately secured. We reglued these tags before using them. We also examined the metal dart tags prior to their use. In general, they appeared to be trouble free. Several orders of both types of tags were used during the course of this study. We were unable to correlate changes in the shedding rates with the specific batch of tags that were used. The shelf life of the plastic used in the tags may be another factor. In some instances we used tags which were manufactured several years before their actual use. Since there were no changes in the tagging method, this reason was discounted. Tagging occurred throughout the purse seine fishing season during 1971, 1973, and 1974, and at the end of the season during 1972, 1975, 1976, and 1977. We do not see why this would have more of an effect on one type of tag than on the other.

Summary and Conclusions

Return data for double-tagged northwestern Atlantic bluefin tuna were used to estimate the shedding rates of plastic and metal dart tags. No significant difference was found between the return rates of the plastic and metal tags when the data were tested for all years combined, but plastic tags appeared to have lower shedding rates than metal tags in most cases. We believe that the combining of the data of all years together (1971-77) probably yields a reasonable approximation to the

average shedding rate for each type of tag. Type-I shedding, which occurs immediately after release, was estimated to be 0.040 for plastic and metal dart tags combined. Type-II (instantaneous) shedding was estimated to be 0.205 for plastic and metal tags combined on an annual basis.

The shedding rates for each type of tag were found to vary over the time period studied, and deviations from the assumption of constant shedding throughout the life of the tagged fish were noted. Due to these differences, one should not be satisfied with the results of one double-tagging experiment. We recommend that double tagging be employed whenever possible, as long as shedding occurs and the rate of shedding is found to vary. Also, tagged fish, especially the ones which have been at liberty for a long time, are more likely to continue to carry at least one tag if they were originally double tagged. The ones that do not continue to carry at least one tag are of no value. Furthermore, relative to the errors inherent in a study of this type we do not feel that there is really any important difference in shedding rates between the plastic and metal dart tags.

Since shedding may increase with time from release, extrapolations based on the assumption of constant L should be made with caution. Also because the tag shedding rates that we found are considerable, efforts should be made to develop a more efficient type of tag with a lower rate of shedding.

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INFLUENCE OF LITTLE GOOSE DAM ON UPSTREAM MOVEMENTS OF ADULT CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*

A major environmental and economic concern in the Pacific Northwest is the continuing decline in the numbers of Columbia and Snake River salmonids. Several investigators (Johnson 1960 and others) have used biotelemetry to study effects of hydroelectric dams (Figure 1) on the upstream movements of adult salmonids. Results indicated upstream movements were delayed at Bonneville (Schoning and Johnson[1]; Monan and Liscom[2, 3, 4, 5]),

[1]Schoning, R. W., and D. R. Johnson. 1956. A measured delay in the migration of adult chinook salmon at Bonneville Dam on the Columbia River. Fish. Comm. Oreg., Contrib. No. 23, 16 p.

[2]Monan, G. E., and K. L. Liscom. 1971. Final report, radio tracking of adult spring chinook salmon below Bonneville Dam,

FIGURE 1.—Location of Columbia and Snake River hydroelectric dams.

the Dalles (Monan and Liscom see footnote 3), and Rock Island (French and Wahle 1956) Dams on the Columbia River and at Lower Monumental (Monan and Liscom[6]; Gray and Haynes[7]) and Lower Granite (Liscom and Monan[8]) Dams on the Snake River. However, delays of upstream migrants were generally not considered excessive. We used radiotelemetry to evaluate effects of Little Goose Dam on upstream movements of chinook salmon, *Oncorhynchus tshawytscha*, in the lower Snake River, and compared our results with those of previous studies at other dams.

Materials and Methods

Our telemetry equipment was developed at the Bioelectronics Laboratory, University of Minnesota (Tester and Siniff[9]; Winter et al.[10]). Transmitters were pressure-sensitive and permitted determination of salmon location and swim-

1971. Northwest Fisheries Center, Natl. Mar. Fish. Serv., NOAA, Seattle, Wash., 24 p.

[3]Monan, G. E., and K. L. Liscom. 1973. Final report, radio tracking of adult spring chinook salmon below Bonneville and the Dalles Dams, 1972. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, 37 p.

[4]Monan, G. E., and K. L. Liscom. 1974. Radio tracking studies of fall chinook salmon to determine effect of peaking on passage at Bonneville Dam, 1973. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, 28 p.

[5]Monan, G. E., and K. L. Liscom. 1975. Final report, radio tracking studies to determine the effect of spillway deflectors and fallback on adult chinook salmon and steelhead trout at Bonneville Dam, 1974. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, 38 p.

[6]Monan, G. E., and K. L. Liscom. 1974. Final report, radio tracking of spring chinook salmon to determine effect of spillway deflectors on passage at Lower Monumental Dam, 1973. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, 20 p.

[7]Gray, R. H., and J. M. Haynes. 1976. Upstream movement of adult salmonids in relation to gas supersaturated water. *In* Pacific Northwest Laboratory Annual Report for 1975, p. 73-76. Vol. I, Life Sciences, Part 2, Ecological Sciences. Battelle, Pacific Northwest Laboratories, Richland, Wash.

[8]Liscom, K. L., and G. E. Monan. 1976. Final report, radio tracking studies to evaluate the effects of the spillway deflectors at Lower Granite Dam on adult fish passage, 1975. Northwest Fish. Cent., Natl. Mar. Fish Serv., NOAA, Seattle, 18 p.

[9]Tester, J. R., and D. B. Siniff. 1976. Vertebrate behavior and ecology progress report for period July 1, 1975-June 30, 1976. COO-1332-123. Prepared for U.S. Energy Research and Development Administration. Contract No. E(11-1)-1332. University of Minnesota, Minneapolis, 63 p.

[10]Winter, J. D., V. B. Kuechle, D. B. Siniff, and J. R. Tester. 1978. Equipment and methods for radio tracking freshwater fish. Univ. Minn. Agric. Exp. Stn. Misc. Rep. 152-1978, 18 p.

ming depth (Gray and Haynes 1977). Transmitters were individually identifiable and operated on a carrier frequency of 53 MHz. Transmitter range varied with depth and transmitter orientation to a receiving antenna. Transmitter life was 2-3 wk. Receivers were capable of distinguishing 100 discrete crystal-tuned transmitters.

Transmitters used in spring 1976 weighed about 68 g in water and were 11.5 cm long and 2.7 cm in diameter. Transmitters used in 1977 were about one-half the weight and two-thirds the volume of those used initially, weighed about 34 g in water, and were 7.9 cm long and 1.9 cm in diameter. In spring 1976 and 1977, chinook salmon were trapped, anesthetized (tricaine methanesulfonate-quinaldine), and tagged externally with radio and metal-core anchor tags (experimental) or metal-core anchor tags only (controls). Tagging was accomplished in cooperation with the National Marine Fisheries Service (NMFS) at Little Goose Dam. Methods of external tag attachment were reported by Gray and Haynes (1977). After tagging, salmon were transported 6.4 km downstream and released at Texas Rapids (Figure 1).

Total lengths and weights of tagged salmon ranged from 66 to 100 cm and 3.4 to 11.4 kg and were consistent with the sizes of fish used in other Columbia River studies (Monan and Liscom see footnotes 2-6). Fish movements between Lower Monumental and Lower Granite Dams (Figure 1) were monitored day and night for the duration of transmitter life. Tagged fish passing through fish ladders at Little Goose and Lower Granite Dams were automatically diverted into fish traps by a magnetometer-triggered device (Durkin et al. 1969), or observed and recorded at fish-counting windows. This allowed comparison of travel time data for control and experimental fish. Total distance traveled was calculated for each fish by summing movements between successive locations.

Results and Discussion

Extensive timing variability among individual salmon was common throughout the study. However, travel times of salmon carrying external radio transmitters and control fish were not significantly different (Gray and Haynes 1979). Average passage delays at Little Goose Dam for radio-tagged and control salmon (combined) were 216±210 h (n=45) in 1976 and 90±57 h (n= 48) in 1977 (Table 1). Passage delays for the same fish at Lower Granite Dam were <50 ±19 h (n = 3) in 1976 and 58 ±45 h (n = 18) in 1977.

While our observations of delay at Lower Granite Dam were consistent with previous research at other Columbia and Snake River Dams (Table 1), it appears that excessive delays occurred at Little Goose Dam, especially in 1976. Differences in passage times at Little Goose Dam compared with other dams (Table 1) were significant (P<0.05, Mann-Whitney test).

Several observations indicate extensive salmon

TABLE 1.—Delay of tagged adult chinook salmon below Columbia and Snake River Dams.

Dam	Study year(s)	Citation	Tag type[1]	No. of fish	Time[2] (h) Mean	Range
Bonneville	1948	Schoning and Johnson (text footnote 1)	NT	35	67	62-72
Bonneville	1971	Monan and Liscom (text footnote 2)	R	20	[3]>63	4-86
Bonneville	1972	Monan and Liscom (text footnote 3)	R	20	141	11-408
Bonneville	1973	Monan and Liscom (text footnote 4)	R	52	[4]<96	24-384
Bonneville	1974	Monan and Liscom (text footnote 5)	R	42	54	3-540
The Dalles	1972	Monan and Liscom (text footnote 3)	R	30	33	4-69
Rock Island	1954-56	French and Wahle (1956)	NT	2,217	72	48-96
Lower Monumental	1973	Monan and Liscom (text footnote 6)	R	20	62	—
Lower Monumental	1975	Gray and Haynes (text footnote 7)	R	20	18	2-42
Little Goose	1975	Gray and Haynes (text footnote 7)	R	10	139	20-288
Little Goose	1976	This study	R, NT	45	216	44-858
Little Goose	1977	This Study	R, NT	48	90	23-212
Lower Granite	1975	Liscom and Monan (text footnote 8)	R	30	78	—
Lower Granite	1976	This study	R	3	<50	35-72
Lower Granite	1977	This study	R	18	58	2-145
Average passage delays, h:						
Little Goose Dam					148.3±63.5	
Other dams					66.0±31.0	
All dams					82.5±49.9	

[1]R = radio transmitter; NT = nontelemetering fish tag.
[2]Values averaged over all fish used in a study.
[3]Time spent in fish ladders only.
[4]Time from release 6.4 km downstream to dam passage.

delays occurred below Little Goose Dam. Radio-tagged salmon travelled mean distances of 26.5 km in 1976 and 42.0 km in 1977 before crossing Little Goose Dam, despite its location only 6.4 km above the Texas Rapids release site. Dropbacks after arrival of fish in the Little Goose Dam spill were common, averaging 1 or 2/fish. Delay times and distances ranged up to 100 h and 40 km/dropback episode. Radio-tagged (1976-77) salmon exhibited three movement patterns after release at Texas Rapids until arrival at Little Goose Dam: 31% (12/39) moved to the dam within 4 to 12 h; 31% (12/39) remained within ±5 km of the release point overnight and moved to the dam the next day; and 38% (15/39) moved downstream as far as 32 km, and then upstream to the dam 1-6 days later.

Once an individual salmon began moving upstream, it traveled 2-5 km/h and, generally, did not stop until reaching Little Goose Dam. After entry into the dam spill, three behavior patterns were observed: 34% (12/35) crossed the dam 2-5 days after release without dropping back; 40% (14/35) crossed the dam after averaging 1.6 dropbacks/fish; and 26% (9/35) were not observed or recorded crossing Little Goose Dam. However, at least four salmon in the latter group were observed passing Lower Granite Dam or were recovered upstream by anglers or at hatcheries, and properly belong in the second group.

At Little Goose Dam, especially with continuous spring 1976 spilling, salmon appeared "confused." Movements to and from the spill area were common. Substantial milling, previously reported at Lower Granite Dam (Liscom and Monan see footnote 8), occurred in a large back eddy on the north side of Little Goose Dam in 1976 and in front of turbine outflows in 1977. Salmon may use rheotactic, olfactory and/or acoustical cues to navigate upstream (Harden Jones 1968). These cues may be distorted by continuous and heavy spilling near dams. Milling may be an attempt to relocate orientation cues (Hasler et al. 1978). In both study years movements into the fish ladder were frequent, but salmon frequently fell back and returned to the spilling basin, especially upon nearing the trapping facility in midladder.

Periodically, fish trapping operations were halted to allow large groups of salmon, which were suspected of accumulating in the spill to pass Little Goose Dam (Slatick[11]). From 26 April to 30 May 1977, the trap was inoperative 17% of the time (6 of 35 days). However, 30% of all salmon counted (7,382 of 24,238) at the fish viewing window by NMFS personnel and 59% (16/27) of our tagged salmon crossed Little Goose Dam during nontrapping periods. Daily viewing window counts of salmon passage averaged 562±497 fish during trapping and 1,230±1,040 fish during nontrapping periods. A t-test showed these differences were significant ($P<0.05$) and indicated trapping operations at Little Goose Dam impeded chinook salmon passage.

Other aspects of dam operations affected salmon passage at Little Goose Dam. One morning in May 1976, spillways were closed for several hours. The five radio-tagged salmon present left the spill and moved downstream as far as 16 km. During the 24 h after spilling was restored, fish returned to the dam. In the absence of spilling in spring 1977, radio-tagged salmon moved into turbulent areas created by water leaving power generating turbines at Little Goose and Lower Granite Dams. When turbine operations were altered, in response to power generation demands, salmon generally exited the area and returned after water-flow conditions stabilized. Salmon passage through the fish ladder was also impeded by turbine operations (Slatick see footnote 11). Finally, the fish ladder at Little Goose Dam uses pumped river water rather than a gravity flow. Of all salmonid species studied, chinook salmon may be most sensitive to and least likely to swim through pumped water (Slatick see footnote 11).

Gray and Haynes (1977) showed that mean swimming depths of adult chinook salmon in the Snake River were significantly greater ($P<0.05$) in spring 1976 than in spring 1977. However, in both years, mean swimming depths in the Little Goose Dam spill were significantly greater ($P<0.05$) than in all other sections of the study area (Haynes 1978). In contrast, swimming depths in the Lower Granite Dam spill were similar to those in the open river between dams. As delays increased in the Little Goose Dam spill, salmon swimming depths increased. Since fish ladder entrances are near the surface, this decreased opportunities for passage.

Although some delays may have resulted from tagging, we believe other factors caused the extensive delays observed at Little Goose Dam. First, our radio-tagged and control salmon had similar passage times at Little Goose and Lower Granite

[11]E. Slatick, National Marine Fisheries Service, Little Goose Dam, Starbuck, Wash., pers. commun. 1977.

Dams in 1976 and 1977 (Gray and Haynes 1979). Second, the 63% passage of internally radio-tagged salmon in 113 h observed by Liscom and Monan (see footnote 8) at Lower Granite Dam was similar to the 69% passage of radio-tagged salmon in 106 h that we observed in spring 1977 for fish that crossed Little Goose Dam or were initially released above it (Haynes 1978).

Our studies provide the first information on salmon movements near Little Goose Dam. Although they affected salmon movements, spilling and turbine operations are regular events at all dams and would not appear to be solely responsible for excessive delays occurring at Little Goose Dam. Fish passage delays may have resulted from tagged salmon being forced to retravel a portion of their migratory route after release. However, tagging and transport stresses, per se, are common to all tagging studies. Our salmon (1976-77) moved to Little Goose Dam in an average of 38 h, a figure consistent with similar studies at Bonneville Dam (Monan and Liscom see footnotes 2-5). Thus, our tagging and handling methods would not appear to be responsible for extensive delays of salmon movements upstream.

Dropback and milling of radio-tagged salmon in the Snake River at Little Goose Dam may be related to salmon trapping operations. Two factors that may contribute to trapping effects are the mechanical aspects of the trap itself and the possible olfactory sensing of trapped salmon by other salmon moving up the fish ladder. Trap entrances are narrow and steep, the trap emits sharp noises when operating, and hydraulic fluid may reach the fish ladder. It is well known that a human hand in the water of a fish ladder can interrupt salmon movement. Many authors (Hasler et al. 1978) have demonstrated great olfactory sensitivity among salmon. The presence of trapped salmon upstream and other disturbances may inhibit salmon passage through fish ladders.

Extensive passage delays, due to dropback and milling and greater swimming depths in the spill below the dam indicate a unique effect of Little Goose Dam on the upstream migration of chinook salmon. We observed delays at Little Goose Dam averaging 148±64 h (Table 1). Delays reported at other dams were significantly less ($P<0.05$) and averaged only 66±31 h. Cause for great concern is the 83±50 h average delay salmon encounter at each dam while migrating through the Columbia and Snake Rivers. Many salmon must pass eight dams (Figure 1) to reach home spawning areas, and the additive effects of a 4 wk, multidam passage delay may significantly influence spawning success, especially in fall run chinook salmon which have shown the greatest decline in numbers. From 1962 to 1969, before Little Goose Dam was operational, annual passage of fall chinook salmon at Ice Harbor Dam averaged nearly 18,000 fish (U.S. Army Corps of Engineers[12]). However, in 1976 and 1977 fall chinook salmon passage at Ice Harbor Dam was only 1,474 and 1,956 fish (U.S. Army Corps of Engineers[13, 14]). Little Goose Dam is 95 km upriver from Ice Harbor Dam (Figure 1). Since the position of fishways, navigation locks, and spillways is different at each dam, effects of each dam must be studied independently. Only then can methods be devised to increase passage success throughout the river system.

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MATURITY, SPAWNING, AND FECUNDITY OF ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, OCCURRING NORTH OF CAPE HATTERAS, NORTH CAROLINA

The Atlantic croaker, *Micropogonias undulatus*, is an important inshore, bottom fish ranging from the Gulf of Maine to Bay of Campeche, Mexico (Chao 1978). United States commercial landings have reached 50,000 metric tons (t) in recent years (Gutherz et al. 1975; McHugh 1977), though dramatic declines in landings have occurred; at least in the area from Cape Hatteras, N.C., to Cape Cod, Mass. (Joseph 1972). White and Chittenden (1977) have postulated the existence of an abrupt change in life histories and population dynamics of Atlantic croaker and other species whose ranges traverse Cape Hatteras. They showed differences in spawning times, size at maturity, maximum size and age, and total annual mortality rates of Atlantic croakers from north and south of Cape Hatteras and speculated the differences may result from different temperature regimes.

Few studies exist on reproduction of Atlantic croaker occurring north of Cape Hatteras. Wallace (1940) studied size at maturity and sexual development of fish from Chesapeake Bay and ocean waters off Virginia and North Carolina. Welsh and Breder (1923) reported size and age at maturity based on collections from Massachusetts to Florida. Occurrence of larval stages and gonad development indicated that spawning occurred from July through December and peaked during October and November (Welsh and Breder 1923; Hildebrand and Schroeder 1928; Wallace 1940). Haven (1957) and Chao and Musick (1977) found indications from juvenile length frequencies of late winter or early spring spawning. The only report of fecundity was that a 395 mm female contained approximately 180,000 eggs (Hildebrand and Schroeder 1928).

This paper presents size at maturity, spawning times as indicated by ovarian development, and fecundity observations of the Atlantic croaker population north of Cape Hatteras.

Methods

All fish were collected during seven National Marine Fisheries Service bottom-trawl surveys of the continental shelf from Cape Hatteras to Block Island, R.I., during 1973-76 (Table 1). The survey design and sampling methods were described by Grosslein (1969). Atlantic croakers were captured each year between lat. 39°00′ N (Cape May, N.J.) and 35°15′ N (Cape Hatteras) in depths from 7 to 131 m.

Subsamples of approximately 25 fish, representative of the length frequency of each catch, were frozen whole for laboratory examination. Each fish was weighed (grams), measured (millimeters total length, TL), sexed, and its maturity stage was determined using the sexual development classification and criteria of Wallace (1940).

TABLE 1.—Summary of Atlantic croaker data collected between Cape May, N.J., and Cape Hatteras, N.C., during 1973-76.

Collection no.	Dates	No. of observations	Number used in probit analysis	
			Males	Females
1	9-16 Oct. 1973	556	245	288
2	27-30 Sept. 1974	699	324	258
3	16-18 Sept. 1975	79	31	28
4	30 Oct.-6 Nov. 1975	607	204	145
5	14-17 Dec. 1975	122	—	—
6	6-17 Oct. 1976	438	84	103
7	18 Dec. 1976	16	—	—
Total		2,517	888	820

Ovaries in development stage 4 from 1973 and 1974 cruises were exsected, weighed (±0.01 g), and preserved in a modified Gilson's fluid (Simpson 1951) for subsequent fecundity estimation.

Egg counts for fecundity estimation were made by a method similar to Bagenal's (1957), but modified as follows. After 4-6 wk preservation the ovaries were washed over a 1.0 mm mesh screen which permitted all the eggs to pass through it but retained the ovarian tissue. After repeated washings and decanting the eggs were diluted in water to a known volume, randomly stirred, and three 10 ml aliquots, each containing from 200 to 400 eggs, were extracted and the eggs counted using a microscope. To test the accuracy of the sampling method two aliquots were extracted from an egg batch, counted, and replaced until 20 aliquots were counted. The mean and standard deviation (SD) of all counts was 255 and 38.3, and the coefficient of variation (CV) was 15.0%. For the means of three samples the SD was 20.4 and the CV was 8.7%. The mean egg number of the three aliquots times the total dilution volume divided by the aliquot volume was used to estimate fecundity.

Estimates of length at maturity (length at which 50% are mature = L_{50}) were calculated using probit analysis (Finney 1971). Samples used in this analysis were collected from September to November (Table 1; cruises 1-4, 6) which minimizes the affects of seasonal growth on length at maturity. The proportion of mature fish for each centimeter group was calculated for each year by sex. Table 2 shows the proportion mature by centimeter group for the interval between 0 and 100% mature. The proportions were transformed to probits (Fisher and Yates 1964) and the iterative method was used to calculate the weighted linear regression equation, $Y = a + b\,X$, by least squares for the logarithm (base 10) of length (X) and the probit (Y). Chi-square tests indicated no significant ($\chi^2_{0.01}$) heterogeneous deviations from the regression lines; therefore, the regression coefficients were used to determine L_{50}. The variance of L_{50} was estimated as:

$$V(L_{50}) = \frac{1}{b^2}\left[\frac{1}{\Sigma nw} + \frac{\left(L_{50} - \frac{\Sigma nwx}{\Sigma nw}\right)^2}{\Sigma nw\left(x - \frac{\Sigma nwx}{\Sigma nw}\right)^2}\right]$$

where n is the number of observations at each centimeter group, w is the weighting coefficient (Z^2/PQ) (Finney 1971, table II) for probit (Y), and x is the logarithm (base 10) of the length.

In order to test for differences in L_{50} between sexes and between years, z-values (Natrella 1966) were calculated using the equation:

$$z = \frac{L_{50_1} - L_{50_2}}{\sqrt{V(L_{50_1}) + V(L_{50_1})}}.$$

TABLE 2.—Percentage mature used in probit analysis by total length group for male (M) and female (F) Atlantic croaker collected in 1973-76. N = number of specimens, L_{50} = length at 50% mature, $V(L_{50})$ = variance of L_{50}, and χ^2 = for goodness of fit of probit regression line.

Total length (cm)	1973		1974		1975		1976	
	M	F	M	F	M	F	M	F
16							0	
17		0			0		17	0
18	0	10	0		16	0	13	31
19	17	29	9	0	18	10	67	70
20	69	45	36	10	37	33	89	80
21	90	86	47	23	32	28	91	85
22	94	84	56	35	47	30	90	83
23	89	78	65	47	50	27	100	71
24	92	86	85	74	47	43		94
25	97	94	95	93	78	69		100
26	100	97	98	97	77	79		
27		100	100	100	90	82		
28					93	100		
29					100			
N	245	286	324	258	235	173	84	103
L_{50}	19.17	19.81	21.57	22.70	22.35	23.27	18.71	18.52
$V(L_{50})$	0.0190	0.0191	0.0357	0.0283	0.0376	0.0356	0.0438	0.0234
χ^2	15.82	13.82	5.11	3.97	7.07	12.16	4.09	8.66
df	7	9	8	7	11	9	6	7

Results and Discussion

Length at Maturity

The matrix of z-values is shown in Table 3. Highly significant ($z>2.33$, $P\leq0.01$) differences were found between sexes within years for 1975 and 1976 and between years for each sex except 1973 and 1976 males and 1974 and 1975 females. This indicates that L_{50} for males and females was greater in 1974 and 1975 than in 1973 and 1976. The greatest difference was found between 1975 and 1976 when L_{50} decreased approximately 4.8 cm for females and 3.6 cm for males.

Significant long-term changes in L_{50} have occurred since Wallace's (1940) studies of Chesapeake Bay croakers. The smallest mature female he observed during 1938-40 was 27.5 cm, indicating a L_{50} of at least 30 cm. His collections were made during July and August; therefore, due to additional growth during early fall, 30 cm is an underestimation of L_{50} for comparison with my results obtained from September-November.

Spawning

The percentage frequencies of maturity stages indicate spawning commenced at least as early as the beginning of September, peaked during October, and ended by late December. The maturity stages and sample years were combined for analysis (Table 4). The percentage of ripe ovaries remained high during September and October, then dropped to a low level in November. No ripe females were found in December. As would be expected the percentage of spawned fish (partially spent, spent, and resting) increased during the sampling period and indicated spawning was nearly completed by mid-December. Because of difficulty in assigning a specific maturity stage to testes and since ovarian development was the best indicator of spawning, males were not analyzed.

The beginning of the spawning season was not sampled; however, an examination of Wallace's (1940) maturity stage data for July and August showed that over 50% of the ovaries were developing (stages II and III) and <10% were ripe (stage IV). The remainder was classified as resting (stage I). Wallace made additional collections in November which showed that ovaries were either partially spent (stage VI) or spent (stage VII). His findings support this study, indicating that spawning commenced about mid-August and was completed by the end of December.

The presence of small juveniles (20-40 mm TL) during April and May have led to speculations of different spawning populations and a spring spawning peak. Chao and Musick (1977) apparently detected a modal group "entering" the York River in May and suggested they may represent

TABLE 3.—Matrix of z-values (Natrella 1966) and significance for differences in L_{50} (length at which 50% of specimens were mature) of male (M) and female (F) Atlantic croaker collected in 1973-76.

	1973		1974		1975		1976	
	M	F	M	F	M	F	M	F
1973 M		0.196	7.269**	16.214**	9.632**	17.546**	6.937**	5.779**
F				9.058**		7.544**		3.196**
1974 M				4.467**	2.903*	6.367**	6.329**	12.546**
F						1.400		12.122**
1975 M						3.400**	8.055**	15.507**
F								9.972**
1976 M								0.729

*$P\leq0.01$; **$P\leq0.001$.

TABLE 4.—Percentage frequency of maturity stages of female Atlantic croaker collected between Cape May, N.J., and Cape Hatteras, N.C., during 1973-76.

		Sampling interval				
Maturity stage	Wallace's stages (1940)	16-18 Sept. 1975	29 Sept.-1 Oct. 1974	5-20 Oct. 1973, 1976	30 Oct.-6 Nov. 1975	14-17 Dec. 1975
Developing	II and III	51	29	23		
Ripe	IV and V	46	51	41	12	
Partially spent	VI	3	7	13	31	10
Spent	VII		11	17	32	28
Resting	I		2	6	25	62
Total		42	286	448	196	51

progeny from a different spawning population. Haven (1957) found 20-30 mm fish during April and concluded the spawning season extended over almost the entire year with a possible spring peak. The apparent 9- or 10-mo spawning season may result from little or no overwinter growth or sampling bias due to differential size distribution or trawl avoidance (Haven 1957; White and Chittenden 1977; Chao and Musick 1977). Maturity observations made during this study showed essentially all adult fish spawned during August through December and it is unlikely a spring spawning peak would occur from the Atlantic croaker population north of Cape Hatteras.

Fecundity

Fecundity ranged from 100,800 to 1,742,000 for fish from 196 to 390 mm TL. Preliminary plots of fish length versus fecundity indicated a curvilinear relationship and plots of fish weight and ovary weight versus fecundity appeared linearly related. Therefore, fish length and fecundity were transformed to logarithms (base 10) and least squares regression lines fitted to the data by year using the equation log fecundity = $\log a + b$ (log length). Fish weight and ovary weight versus fecundity were related by the linear regression equation $Y = a + bX$ where Y is fecundity and X is either fish weight or ovary weight. Analysis of variance indicated no significant ($P \leq 0.05$) differences in variance about the regression between years for each of fecundity versus length, weight or ovary weight. Analysis of covariance was used to test for between years differences in fecundity relationship. No significant ($P = 0.01$) difference was indicated; therefore, regression equations were calculated for pooled data. Scatter diagrams and fitted lines are shown in Figures 1-3.

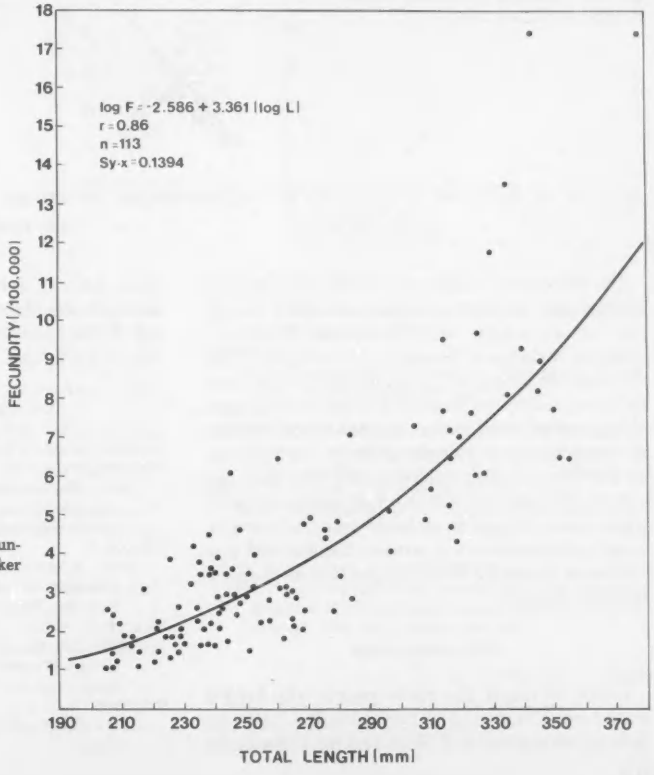

FIGURE 1.—Relationship between fecundity and total length for Atlantic croaker collected in 1973 and 1974.

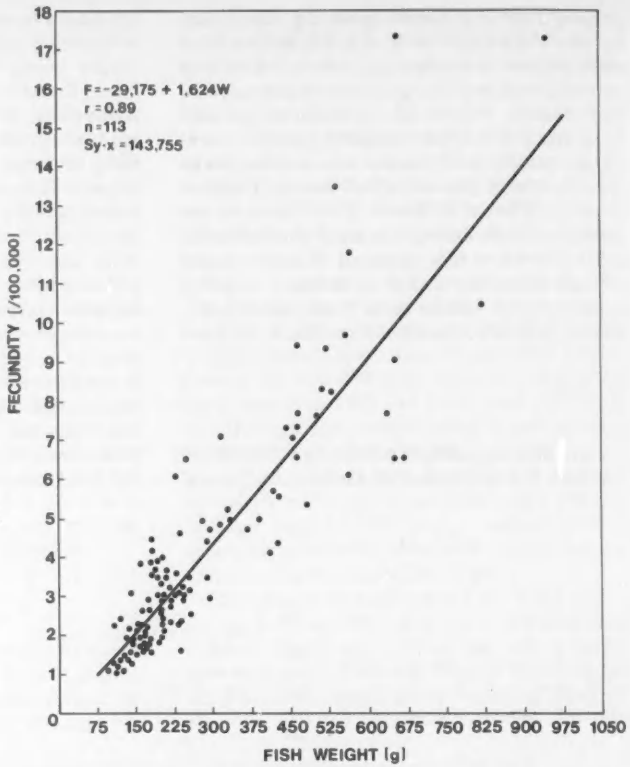

FIGURE 2.—Relationship between fecundity and fish weight for Atlantic croaker collected in 1973 and 1974.

The correlation coefficients for the relationships of fecundity to length, weight, and ovary weight show ovary weight was most closely associated with the variation of fecundity. Unless the ovaries are selected, however, ovary weight is the least reliable predictor of fecundity. It is the most variable parameter and, unless ovaries are collected at the penultimate development stage, the relationship of ovary weight and fecundity will vary seasonally. Fish weight will also vary seasonally and, when ovary weight is included with fish weight, some autocorrelation is present. For general prediction of fecundity, length appears to be the most reliable measure.

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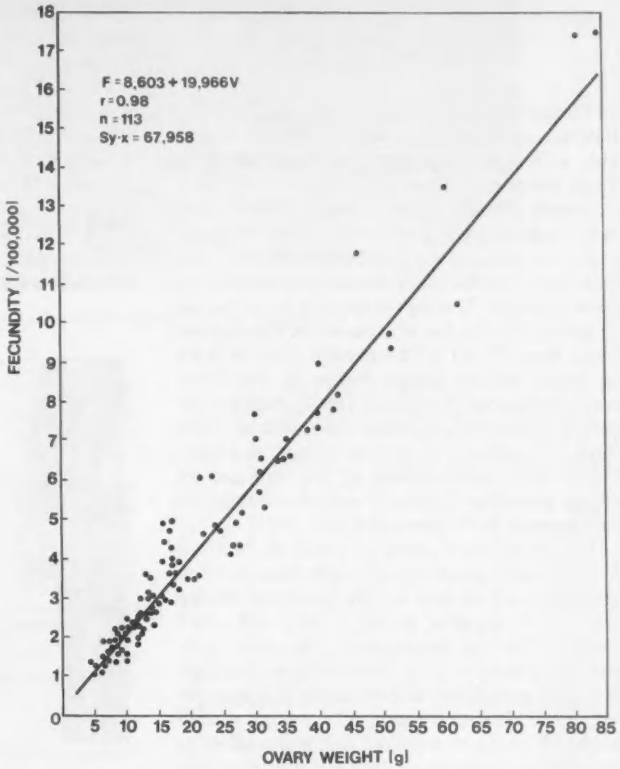

FIGURE 3.—Relationship between fecundity and ovary weight for Atlantic croaker collected in 1973 and 1974.

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COMPARISON OF SAMPLING DEVICES FOR THE JUVENILE BLUE CRAB, *CALLINECTES SAPIDUS*[1]

The behavior of the blue crab, *Callinectes sapidus* Rathbun, in the Chesapeake Bay varies considerably with age, temperature, and molting cycle. These behavioral differences make efforts difficult to sample effectively the population densities in the Chesapeake Bay and its tributaries. No single gear type appears to sample effectively the blue crab during winter and summer at all depths and types of bottom. During winter blue crabs burrow in the mud in the deeper channels of Chesapeake Bay (Churchill 1917). This pattern is the basis for an active winter dredge fishery in the lower portion of the bay (Van Engel 1962). During a 3-yr survey of blue crabs, Lippson[2] found that juveniles were also present in deeper waters in winter. Comparative effectiveness of two dredges for winter sampling of juvenile and adult blue crabs was reported by Sulkin and Miller (1975).

Blue crabs move about in relatively shallow water in warm weather presumably because of the abundance of food here and for protection among submerged aquatics while in the soft shell condition. During the summer 7.3 m otter trawls have been found to be an effective gear to sample the adult population of blue crabs (Lippson see footnote 2). The otter trawl, with a small stretch mesh (0.6 cm) liner in the cod end, is also effective for catching juveniles in deeper water; however, juveniles spend much of their time in shallow waters during the warmer months. The push net (Figure 1), beach seine, and small otter trawls have all been used with some degree of success in this shallow region.

It is the purpose of this study to compare the effectiveness of the push net, otter trawl, and crab scrape (Figure 2) in catching juvenile blue crabs in shallow water.

Methods and Results

Smith Island in the Chesapeake Bay has extensive grassy (*Zostera marina*) beds which are ideal habitats for juvenile crabs (Stevenson and Confer 1978). This region was chosen to compare the catch effectiveness among a 3.7 m otter trawl, 81.3 cm push net, and a 96.5 cm modified crab scrape during summer 1975.

The otter trawl opened to a working width of 3.6 m. The gear was towed by the RV *Chelae* in depths of 1-2 m for 0.7 km. The cod end was lined with 0.6 cm stretch mesh netting. The trawl door size was 30.5 cm × 61.0 cm and the length of the bridle was 45.7 m.

The push net had a steel frame 81.3 cm wide and 60.9 cm high fitted with a 0.6 cm stretch mesh bag. The leading edge had a 7.6 cm diameter pipe which

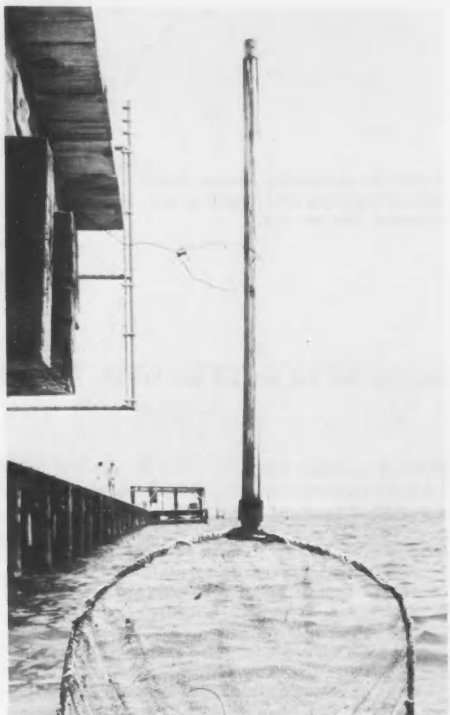

FIGURE 1.—Push net used for blue crab fishing with the roller bar on the leading edge.

[1]Contribution No. 992HPEL from the Center for Environmental and Estuarine Studies, University of Maryland.

[2]Lippson, R. L. 1969. Blue crab study in Chesapeake Bay-Maryland. Nat. Resour. Inst. Q. Prog. Rep. 3, Ref. No. 69-33B:1-13.

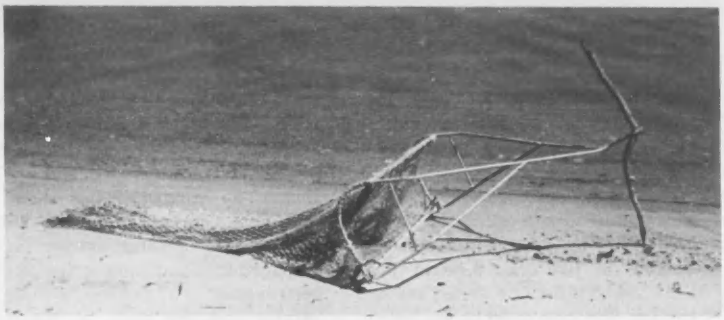

FIGURE 2.—The crab scrape used for blue crab fishing.

rolled over the bottom. The handle was 1.5 m long. The net was manually pushed along a 0.7 km course, waist to chest deep, and parallel to the shoreline.

The crab scrape, used commercially for catching shedding crabs, had a metal frame 96.5 cm wide and 38.1 cm high. The lead bar on the crab scrape has no teeth, a basic difference between it and a dredge. A 3.8 cm twine net 182.9 cm long was fitted to this frame. The crab scrape is towed from a shallow-draft boat over grassy beds. The crab scrape used in this study was modified by fitting it with a 0.6 cm stretch mesh net to retain small (>3 mm) crabs.

The otter trawl and crab scrape were towed simultaneously beside each other from two small outboard motorboats for 6 min at an engine speed of 2,000 r/min. The push net was then pushed parallel to the trawl and crab scrape tows over the same distance but closer to shore. The depths for the trawl and crab scrape tows ranged from 1 to 2 m whereas the push net sampled in depths of 0.6-1.1 m. Eighteen samples were collected for each gear type.

The sex and size class of crabs were determined after each tow. Crab size was determined using carapace width from one lateral spine tip to the other. Crabs >60 mm wide were excluded from consideration in this study because they were not in the most recent year class. Three size classes were used: class I measured 1 to 20.0 mm; class II, 20.1 to 40.0 mm; and class III, 40.1 to 60.0 mm.

The mean number of crabs per square meter is shown in Figure 3. It is apparent that the trawl is comparatively ineffective for classes I and II. The trawl and push net are about equally as effective for class III although neither is as effective as the modified crab scrape for classes I, II, or III. The crab scrape is the most effective gear for sampling juvenile blue crabs.

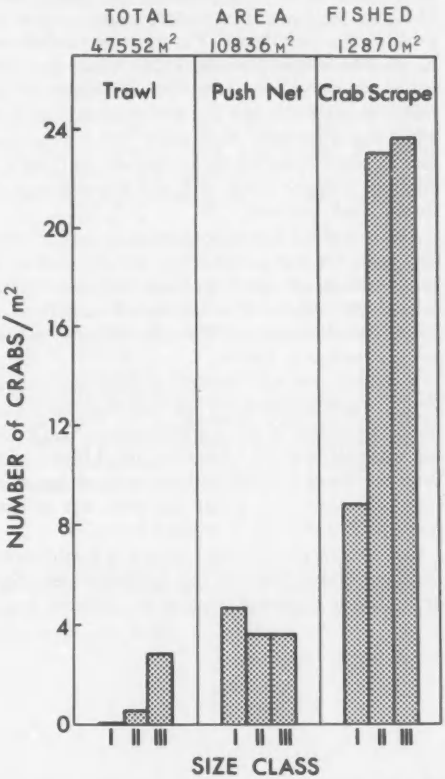

FIGURE 3.—Mean number of blue crabs per square meter for each haul and total area fished by each gear. Size class (carapace width) I = 1-20.0 mm, II = 20.1-40.0 mm, and III = 40.1-60.0 mm.

Discussion

In evaluating various gear for sampling juvenile blue crabs, a variety of factors should be considered, such as catch effectiveness, gear cost, ease of handling, and person hours.

It generally requires two persons to efficiently operate an otter trawl from a small outboard motorboat. Handling an otter trawl from a small outboard motorboat is not only difficult but dangerous as the net can become fouled in the propeller. If the net fills with mud or too much debris, it is impossible to bring the gear on board and the catch must be sacrificed. The push net is operable by one person and snags are infrequent. Mud, as well as high rooted aquatics, makes pushing the net difficult. The push net is effective in shallow water (Strawn 1954). Clear shallow water, however, decreases the effectiveness as many small crabs see the net approaching and swim out of its path (pers. obs.). The crab scrape can be easily handled by one person and seldom becomes snagged (pers. obs. and observations of commercial crabbers).

The cost of a 3.7 m otter trawl is about $150.00. The push net cost varies. They are not available commercially and must be constructed, usually by a local blacksmith. The bag may be cut from a ripped beach seine net. The approximate cost of the crab scrape is $55.00.

Although gear cost, ease of handling, and hours involved are considered in gear selection, the most important factor is catch effectiveness. The push net was more effective catching small blue crabs than the trawl but the modified crab scrape was more effective than either the push net or the trawl when sampling in shallow water.

Considering all pertinent factors, it would seem that the crab scrape is the preferred gear for quantitative studies of juvenile crab abundance.

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